University of Alberta

BRYOPHYTES, LICHENS, AND FUNGI ON DOWNED WOODY MATERIAL IN ASPEN MIXEDWOOD FORESTS OF NORTHEASTERN ALBERTA

BY

Susan F. Crites

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE

IN

PLANT ECOLOGY

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled NONVASCULAR PLANTS ON DOWNED WOODY MATERIAL IN ASPEN MIXEDWOOD FORESTS OF NORTHEASTERN ALBERTA submitted by SUSAN FRANCES CRITES in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE in PLANT ECOLOGY.

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Abstract

This study examined the importance of substrate, stand age, and environmental factors on diversity and abundance of nonvascular species in aspen mixedwood forests. Sampling was carried out on downed woody material (DWM) in young (23-26 years), mature (51-63 years), and old (122-146 years) aspen mixedwood stands. DWM was categorized into one of seven decay stages. Environmental variables including light, pH, and wood type were measured for a subset of DWM. Diversity and abundance of nonvascular species were related to decay stage and stand age. Old stands had the greatest number of species and the greatest diversity of woody substrates in each of the decay stages. Decay stage was the main determinant of variance in the species distributions, followed by stand age, pH, and wood type. These results suggest that assemblages of nonvascular species may be altered if old aspen stands are removed from the forest landscape, and that wood in different stages of decay is important to maintaining such assemblages.

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Chapter I
General Introduction

Northeastern Alberta is embarking on a new era of forest management. Historically, fire was the primary disturbance that affected forest succession in Alberta. A new disturbance regime has recently been introduced to northeastern Alberta. Logging to produce pulp from aspen trees began in northeastern Alberta in 1993. In 1991, the provincial government signed a Forest Management Agreement (FMA) with Alberta-Pacific Forest Industries, Inc. (ALPAC). The agreement allows ALPAC to harvest ~2,500,000 cubic metres of aspen annually in a 6,000,000 ha area. ALPAC has since constructed the largest single-line bleach kraft mill in the world. Historically, Alberta has been dominated by coniferous harvesting, and as a result, little research has examined the effect of harvesting on aspen stands. Research projects initiated in 1992 have recently produced results, leading to management recommendations regarding the future of these forests. Despite boreal mixedwood research, there is still a general lack of knowledge regarding the effect of time on this ecosystem.

Little is known about ecosystem function of bryophyte and lichen communities and the changes that occur within these communities throughout succession (Franklin *et al.* 1981, Canters *et al.* 1991, Lesica *et al.* 1991, Hyvärinen *et al.* 1992). Due to the many morphological factors separating them from vascular plants, sampling difficulties, and difficulties in identification, bryophytes and lichens are largely ignored in ecological studies (Lee and La Roi 1979a, Franklin *et al.* 1981, Synge 1981, Vitt 1991, Bisang and Urmi 1994). Nonvascular species are unique in that their distribution is largely controlled by microclimate, substrate, and time (Muhle and LeBlanc 1975, Lee and La Roi 1979b, Larson 1984). For the purposes of this paper "nonvascular" will be referring to mosses, lichens, liverworts, and fungi (algae will not be included).

Bryophytes and lichens lack a well-developed vascular system, including roots, therefore they cannot withdraw water from substrate in the same manner as vascular plants (Richardson 1981, Kershaw 1985). These constraints have resulted in bryophytes and lichens becoming poikilohydric, that is, they are able to dry out and survive periods of drought (Larson 1984, Kershaw 1985, Vitt *et al.* 1988). They are then able to resume normal metabolic functioning upon rewetting (Richardson 1981, Kershaw 1985). This strategy has enabled bryophytes and lichens to occupy several harsh substrates. That is, there are particular groups of bryophytes and lichens that grow on rocks (saxicolous), living trees (corticolous or epiphytic), logs or decaying wood (lignicolous or epixylic), or on soil or humus (terricolous or humicolous). Many of these substrates are impenetrable

by the roots of vascular plants, enabling nonvascular species to be free from competition by vascular plants for light and nutrients (Richardson 1981, Proctor 1981). Therefore, bryophytes and lichens differ from vascular plants in their substrate preferences and their response to environmental gradients (Lee and La Roi 1979b).

During succession, *Picea glauca* (Moench) Voss develops in the understory of some *Populus tremuloides* Michx. stands of boreal mixedwood forests. In the absence of disturbance, *P. glauca* can eventually dominate the stand as aspen trees become old and succumb to fungal pathogens (Peterson and Peterson 1992). Coincident with canopy changes, light regimes and chemical properties of the soil change, leading to significant changes in understory vegetation. The lush understory that was dominated by many herbs and shrubs, forming various strata, becomes a homogeneous understory dominated by a carpet of bryophytes. These bryophytes largely control the hydrology of such a forest, as well as contributing to total energy flow and nutrient cycling (Tamm 1953, Forman 1969, La Roi and Stringer 1976, Nienstaedt and Zasada 1990, Vitt 1991).

Bryophytes and lichens are unable to grow on the ground of aspen forests because of the thick litter layer present and the blanketing effect of autumn leaf-drop (Longton 1992, Sveinbjörnsson and Oechel 1992). Deciduous litter is rapidly broken down, returning organic material to the soil, producing a well-developed A soil horizon (Lambert and Maycock 1968). This rapid litter turnover does not allow lichens or bryophytes to become established on the forest floor. Therefore, soil is not an important substrate for mosses and lichens in aspen forests. In conifer forests however, there is a slow breakdown of organic matter. Soil is covered by slowly decomposing conifer needles, producing an acidic substrate that some mosses and lichens can not only tolerate, but proliferate in (Lambert and Maycock 1968). In aspen forests, nonvascular species are largely confined to tree bases and downed woody material (DWM) where litter does not prevent growth (Longton 1992). DWM provides a unique substrate, elevating nonvascular species above competition on the forest floor, positioning them where moisture is more readily available in the form of rain or runoff, where the substrate pH may be more favorable than the ground pH (La Roi and Stringer 1976), and where limiting nutrients can be made available to these species (Vitt 1991).

DWM forms a major element of structural diversity in natural forest ecosystems and is an important part of nutrient and organic matter dynamics (Franklin 1993, Keenan *et al.* 1993, Stewart and Burrows 1994). As logs decompose, they pass through different stages of decay. The time required for decay varies with log species, climate, colonizing organisms, and geography (Swift 1977, Harmon 1993). As a log decays the tissues become softer and more nutrients are released to the surroundings, therefore becoming

more suitable for a wider range of plants than it was before it started to decay (Mattson *et al.* 1987, Alban and Pastor 1993, Arthur *et al.* 1993). Bryophytes have the ability to absorb some of these nutrients, and as the logs decompose, the subsequent steady release of these nutrients can be useful for vascular plants such as tree seedlings (Vitt 1991). The gradual decay process produces a temporally unstable substrate for nonvascular species, forcing them into a finite period of growth (Söderström 1988a). It has been demonstrated that unstable substrates are richer in species than stable substrates (La Roi and Stringer 1976). This temporal patchy substrate is said to support opportunistic species with efficient modes of reproduction and dispersal, unlike stable and continuous substrates which are colonized by more abundant 'climax' species that reproduce mainly by vegetative means (La Roi and Stringer 1976). In stands with a high structural complexity, such as, abundant DWM, more microhabitats will exist, leading to high species richness (Gustafsson *et al.* 1992a, Franklin 1993). It has been shown that old deciduous stands have a highly variable topography and DWM distribution, providing biological and functional diversity (Peterson and Peterson 1992).

Many studies have documented that stand age is a critical factor in determining lichen and/or bryophyte diversity (Söderström 1988a, Lesica *et al.* 1991, Gustafsson *et al.* 1992b, Hyvärinen *et al.* 1992, Berg *et al.* 1994, Selva 1994). Due to relatively slow growth rates, it may take many decades for bryophytes and lichens to exhibit high cover and species richness (Larson 1984), and depending on substrates, successful dispersal may be rare (Söderström 1988a, Lesica *et al.* 1991). Furthermore, Berg *et al.* (1994) concluded that for all rare and threatened species in Sweden, the two most important habitat elements were DWM and old deciduous trees. Large old trees are indicative of a long disturbance regime interval. Gustafsson *et al.* (1992a) reported that for bryophyte diversity, a long interval between disturbance events is more important than the mean tree age within the forest. Similarly, Selva (1994) found rare indicator lichen species required old forests that had been present long enough to acquire the variety of microhabitats that enabled these rare species to become established. Once the rarer species have become established, Selva (1994) maintains that they require substrates in various stages of decay, and ecological continuity of the tree layer, to ensure their survival within these old forests. Therefore, tree age is not the only important factor when determining importance of habitat for nonvascular species, there are many other co-variables dependent on tree age that serve to provide suitable habitat. The effects of stand age and substrate on distribution and diversity of nonvascular species have not been examined separately in the literature.

ALPAC uses short-rotation logging (~70 years), therefore many old aspen stands are being brought into rotation to increase younger, more marketable stands (Anonymous

1992), leading to a truncation of the age-class distribution of these forests. This alteration of the age-class distribution will cause a change in the dynamics of DWM. There will be fewer older stands, decreasing the range of decay stages and sizes. Currently, logging companies are striving to recreate many of the structural attributes found in older forests in attempts to approximate natural ecosystems by leaving clumps of live trees, snags, and DWM (Swanson and Franklin 1992). It has been demonstrated that time and a long disturbance regime interval of a forest are important factors for nonvascular plant diversity (Gustafsson *et al.* 1992a, Berg *et al.* 1994, Selva 1994). Therefore, structurally recreated stands may not be able to support many species of bryophytes and lichens that are found in naturally occurring old forests (Söderström 1988a, Lesica *et al.* 1991, Gustafsson *et al.* 1992a, 1992b).

The direct effects of logging on bryophytes, lichens, and fungi may not be readily apparent. This group of organisms is highly dependent upon substrate and microclimate. Logging causes many dramatic changes to an ecosystem that either directly or indirectly affect substrate and microclimate. If suitable substrates are removed from the ecosystem, many species will be unable to reproduce and may be eliminated (Söderström 1988b). Söderström (1988b) concluded that DWM of all stages of decay and of large diameters are important to maintain a rich nonvascular plant flora. In Sweden, 53% of cryptograms and invertebrates that were threatened preferred logs that were in intermediate stages of decay (Berg *et al.* 1994). Managed stands have an uneven supply of DWM in different stages of decay, with some stages missing or rare (Söderström 1988a). Once an area has been logged, the microclimate becomes completely altered. High humidity is known to be important for many nonvascular species (Gustafsson *et al.* 1992a). In natural forests new downed logs are being recruited regularly. If an area is clear-cut logged, there will be few remaining trees that will be able to contribute to the input of downed woody material in the regenerating stand (Söderström 1988a). Shade-tolerant species that were growing on logs under an aspen canopy will be unable to reproduce or will die following logging, if not severely damaged or killed by the logging event itself. Research needs to determine the dependency of nonvascular communities on decay stages and stand age, and to apply such results to forest harvest strategies.

Because nonvascular species must disperse in order to survive on a temporarily existing substrate of downed logs, these species may become isolated due to forest fragmentation. As time proceeds, the area of natural forest will decrease, and remnant forest stands will become isolated in the landscape. Gustafsson *et al.* (1992a, 1992b) found a positive association between sensitive lichen and bryophyte species and stand area. They also found that in areas surrounded by young forest, which is likely to be the

case for much of northeastern Alberta, the young forest was not useful for dispersal. Adjacency is also an important consideration. Whether particular nonvascular species disperse vegetatively or through spore production, there is a greater probability that they will colonize adjacent forests rather than distant forests (Gustafsson *et al.* 1992a). Forest islands, when preserved, can serve as refugia for many species. If conditions are suitable, these islands can serve as centers for dispersal into adjacent newly developing stands. In a natural stand, epixylic species need only to disperse short distances because of the availability of substrates (Söderström 1988a), but in a managed stand, where some decay stages may be missing, species existing on intermediate stages of log decay may be locally extirpated. Colonization in managed stands will depend on the species abilities for spore production and dispersal, and/or dispersal of vegetative reproductive structures, (Söderström 1988a, Lesica *et al.* 1991), the distance spores travel, microclimate of the managed stand and adjacent stands, and the availability of substrate. Many bryophytes and lichens have limited dispersal capabilities, leading to reduced colonization in newly available habitat in a highly fragmented landscape (Lesica *et al.* 1991, Selva 1994).

Land management agencies and the public are now beginning to understand the importance of maintaining biological diversity (Lesica *et al.* 1991). Interest in conservation biology and threatened species has grown in recent years (Berg *et al.* 1994). To manage forests for the protection of biological diversity, we need to understand the extent and nature of dependencies of all component strata and species on various ages of forests (Lesica *et al.* 1991). Berg *et al.* (1994) stated that studies of the biology and distribution of all sensitive organisms in large areas are lacking. It is important that areas of high biological value with unique species assemblages be identified.

This study addresses the following: pattern of nonvascular plant richness and abundance with stand age; pattern of DWM decay in aspen mixedwood stands; nonvascular plant communities within each decay type; similarities/differences in nonvascular plant communities on the same decay stages in different aged stands; successional patterns of nonvascular species; environmental variables influencing nonvascular plant distribution. DWM was categorized into one of seven decay stages, and nonvascular plant communities on the DWM were sampled. Multivariate techniques were used to evaluate whether decay stages consisted of predictable species assemblages. Environmental variables were measured to determine their relative influence on the distribution of nonvascular species.

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Chapter II
Effects of Stand Age and Substrate on Diversity of Nonvascular Species in Aspen Mixedwood Forests of Northeastern Alberta

The "Red Lists" of threatened animals and plants, as defined by the International Union for the Conservation of Nature (1988), classifies species into different categories of threat. In a few countries, Sweden for example, red lists are extensive and there is detailed information on the flora and fauna. Most countries, however, have incomplete red lists, and information about small organisms (bryophytes, lichens, fungi, and invertebrates) is especially lacking (Berg *et al.* 1994). With the increasing emphasis on biodiversity in the last decade, many authors now agree that such knowledge on smaller organisms is essential and long overdue (Franklin *et al.* 1981, Synge 1981, Wilson 1987).

It was not until the advent of logging to produce pulp from aspen trees, that concern developed for species of the boreal forest of Alberta. The vast area that had previously been exploited for oil and gas, agriculture, recreation, and small-scale coniferous harvesting, was now going to have large-scale aspen harvesting added to it. Concerns of this large-scale aspen harvesting damaging the ecosystem have been expressed by many, and are warranted due to the lack of detailed studies and inventories of species living in the boreal forest of Alberta.

The primary substrate of nonvascular (mosses, lichens, liverworts, and fungi; algae are not included in this discussion) plants in aspen mixedwood stands is downed woody material (DWM); therefore, for this study all nonvascular species were sampled on logs. Most studies investigating the composition and structure of nonvascular plant communities on DWM have been based on subjective methods of data collection and weak analysis. The other problem with such investigations of nonvascular plant communities is the lack of information regarding substrate (see Bisang and Urmi 1994, Gustafsson 1994). Much more detailed quantitative work has been done examining bryophyte and lichen patterns on live trees (e.g. Jesberger and Sheard 1973, Slack 1976, John 1992, Gottsberger and Morawetz 1993, Berg *et al.* 1994, Hilmo 1994). The purpose of this study was to compare diversity and abundance of bryophytes, lichens, and fungi on DWM in young, mature, and old aspen mixedwood stands. A secondary purpose was to determine whether there were unique assemblages of nonvascular species on varying decay stages of DWM, and to identify those assemblages in an attempt to understand better how nonvascular species use DWM.

Methods

Study Area

The study area was located in the Mixedwood Section of the Boreal Forest Region of Alberta (Rowe 1972). All stands selected for study were located within the Lac La Biche Forest District (between 54° and 55° north latitude, 111° and 113° west longitude). Elevation of stands varied between 550 - 580 m above sea level. The annual precipitation is 513.5 mm, of which 306.4 mm falls during the growing season from May to September. The average annual temperature is 1.1°C, with winter and summer means of -15.2 and 14.9°C, respectively (Lac La Biche A climate station 54°46'N, 112°1'W; Anonymous 1980). Parent materials for soils developed from local till deposits. Particle size analysis suggests they are sandy clay loam classification. Soils in the study area are classified as luvisolic and brunisolic (Alberta Parks Service 1974).

Stand Description

Three age classes of aspen mixedwood stands were selected for study, young mature, and old (see details below). *Populus tremuloides* Michx. is the dominant tree species in all stands. Older stands have higher abundances of *Picea glauca* Moench (Voss), *Betula papyrifera* Marsh., and *Abies balsamea* (L.) Mill. than young or mature stands. The abundance of *P. tremuloides* decreases with increasing stand age. *Populus balsamifera* L. is present in moderate abundances in most stands.

Common shrubs include *Rosa acicularis* Lindl., *Alnus crispa* (Ait.) Pursh, *Lonicera involucrata* (Richards.) Banks, *Salix* L. spp., *Ribes oxyacanthoides* L., and *Rubus idaeus* L.. Common ground layer vascular plants include *Aralia nudicaulis* L., *Maianthemum canadense* Desf., *Mertensia paniculata* (Ait.) G. Don., *Petasites palmatus* (Ait.) A. Gray., *Galium boreale* L., and *Rubus pubescens* Raf.. The number of tree species, density of conifers, and tree height and diameter increase from young to old stands. Percent cover of shrubs and grasses is higher in young and old stands than in mature stands; the reverse is true for herb cover.

Field Methods

Twelve forest stands of pyrogenic origin were selected for study. Of the twelve stands selected, four were young (23-26 years), four were mature (51-63 years), and four were old (122-146 years). Stands were selected based on Alberta Phase 3 Inventory Data (Alberta Forestry, Lands and Wildlife 1985). Tree cores were obtained from a random sample of canopy trees to determine stand ages. Young stands had a canopy height of 8 - 11 metres, tree density of 5000 - 7000 stems/hectare. Mature stands had a canopy height

of 15 - 20 metres, and a tree density of 1000 - 3000 stems/hectare. Old stands had a canopy height of 20 metres or more and a tree density less than 1000 stems/hectare with many canopy gaps. All stands were greater than 100 hectares in size (with the exception of one stand that was 80 hectares), had no obvious human disturbance (with the exception of oil exploration lines at approximately 1 kilometre intervals), were dominated by *Populus tremuloides*, and were surrounded by a 100 metre - wide unsampled buffer. Mature and old stands were located east of the town of Lac La Biche (54°45' N, 112°30' W), Alberta. Young stands were located southwest of the town of Wandering River (55°20' N, 112°30' W), Alberta. There were no suitable young stands near Lac La Biche. By positioning a 200 x 200 metre grid on aerial photographs of the stands, we randomly selected six 100 metre circular sampling sites within each of the twelve stands. Each site had a 100 metre radius.

At each site, DWM was sampled along four 100 metre transects radiating out from site center. Each transect was random in direction. DWM was sampled using the line intersect method (De Vries 1974). Five random points were selected along each 100 metre transect. DWM was sampled on 5 metre segments along the transect from each of the five points, totaling 25 metres/transect and 100 metres/site. Any DWM greater than 11 centimetres in diameter intersecting the transect was categorized by decay class and diameter.

Decay was divided into seven stages modified from McCullough (1948) as follows: 1) log whole and undecayed, bark, branches, and twigs present and intact, log elevated on support points; 2) log sound, wood hard, twigs mostly lacking, less than 50% of the bark missing; 3) wood soft in places, some branches remaining, 50% or more of the bark missing; 4) little to no bark remaining, no branches, wood soft with small crevices and small pieces lost; 5) large wood fragments lost, outline of trunk slightly deformed, vascular plants beginning to colonize; 6) wood mostly well-decayed, log colonized by various herbs, shrubs, and trees; 7) humification nearly 100%, hard to define as a log, outline indeterminable, no evidence of hard wood.

In the case of logs that had branches crossing the transect, each branch was considered a separate log. Diameter of logs bisecting the transect was taken at the intersection point between log and transect.

Surveys of mosses, lichens, liverworts, and fungi were completed by point sampling. A 5 x 5 centimetre marked grid was placed on the logs. The grid was 30 centimetres in length, and width was dependent on the circumference of the log. The center point of the grid was placed on the log at the intersection point between the log and the transect, and the grid was wrapped around the log, with the length of the grid lying

along the length of the log. All mosses, lichens, liverworts, or fungi at each of a minimum of 21 grid intersections were identified and recorded. Unidentified species were collected and later identified at the University of Alberta. If nonvascular plats were absent from grid points, whatever was occupying the grid point was recorded as; litter, bark, wood, herbs, shrubs, or trees. The number of sampling points/log varied according to the circumference of the log. All DWM was sampled for as much of the circumference as possible above ground surface. DWM was sampled between May 1 and June 1, and between August 10 and September 10, 1992.

Nomenclature generally follows Anderson *et al.* (1990) for mosses, Stotler and Crandall-Stotler (1977) for liverworts, and Gilbertson and Ryvarden (1986), Martin and Alexopoulos (1969), Schalkwijk-Barendsen (1991), Moser (1983), and Abbott and Currah (1989) for fungi. Egan (1987, 1989, 1990, 1991) was used for lichens, with the exception of *Peltigera* species, for which and Goffinet and Hastings (1994) was used.

Fungal species will not be included in most of the discussion because most of the fungi found were typical wood decay fungi and the fungi are extremely underestimated as only fruiting bodies were recorded, the actual number of species of hyphae in DWM were not examined.

Data Analysis

Substrate diversity for each stand age was assessed by examining the range of log diameters and decay stages that were available for colonization. For nonvascular species on logs, gamma diversity was calculated as species richness within each age class. Alpha diversity was assessed by examining the how the number of species in each site varied, and was also calculated with the Shannon Index (Magurran 1988). The number of species found was plotted against the number of occurrences to evaluate the number of common and rare (less frequent) species within each age class.

Species were broken down into three ecological groups (modified from Söderström 1988a): epiphytes (species commonly found on live trees); epixylics (species typical of rotting wood); and terricolous species (species that use the ground as their primary habitat, but can also be found growing on litter, mosses, live tree bases, and/or rotting wood).

To determine whether decay stages of DWM could be separated based on nonvascular species composition and abundance, discriminant analysis was used. Discriminant analysis is a method for analysing group differences on the basis of external measured variables. A stepwise procedure was used that was based on minimizing overall Wilk's lambda. Wilk's lambda is the ratio of within groups sum of squares to total sum of

squares. The significance of the change in Wilk's lambda when a variable is entered or removed from the model can be tested by transforming lambda to a variable that has approximately a chi-square distribution. Initial classification of DWM was based on physical characteristics (i.e., decay stages). This classification was tested against the abundance distribution of nonvascular species (and other variables that may have been present at grid points) across all DWM decay stages. The analysis will exhibit optimal separation of groups based on linear combinations of the measured variables (Williams 1983; SPSS Inc. 1988). Point data for each log was converted into proportions, so that each log had equal representation, irrespective of size.

To test whether log diameter affected species richness, thus biasing the age results, decay stages were grouped based on the discriminant classification, and regression coefficients were calculated among decay groups for each stand age by plotting species richness against log diameter. Analysis of covariance was used to test the hypothesis that the slopes of the species/diameter curves for all three age classes were the same within each decay group (Zar 1984), which would indicate that log size did not influence species richness within a given decay stage.

To determine if the nonvascular community on a log of decay stage four, for example, is the same in all three ages, logs were randomly removed where possible from young, mature, and/or old datasets within each decay stage to produce equal sample sizes of logs. Species richness and composition were then compared across age classes to determine if all decay stage four logs, for example, were colonized by the same nonvascular community regardless of stand age.

To separate decay stage from stand age, pairwise dissimilarity coefficients were calculated using chord distance (Orloci 1978) for each decay stage between the three stand ages. Chord distance (CRD) is calculated by projecting the sampling units (logs) onto a circle of unit radius by using direction cosines. The measure is the chord distance between the two sampling units after the projection (Ludwig and Reynolds 1988). Chord distance is calculated by

$$\mathrm{CRD}_{jk} = \sqrt{2(1 - \mathrm{ccos}_{jk})}$$

where the chord cosine (ccos) is calculated by

$$\mathrm{ccos}_{jk} = \frac{\sum_{i=1}^{S} (X_{ij} X_{ik})}{\sqrt{\sum_{i}^{S} X_{ij}^2 \sum_{i}^{S} X_{ik}^2}}$$

where X_{ij} represents the abundance of the *i*th species in the *j*th sampling unit, and *S* refers to number of species. CRD ranges from 0, if samples are identical, to $\sqrt{2}$ (or 1.41), if samples are maximally dissimilar. Results were normalized to a scale of 0 to 1 by dividing all values by $\sqrt{2}$.

Results

Downed Woody Material

All forest age classes had different diameter class distributions and frequencies of downed woody material (DWM). There were 333, 176, and 317 logs sampled in young, mature, and old stands, respectively. Young stands had the greatest frequency of logs in small diameter classes ranging from 13 to 21 cm (Figure II-1a). In mature stands, the frequency distribution of logs was more even, with the greatest frequency of logs occurring in diameter classes ranging from 21 to 29 cm (Figure II-1b). Old stands were similar to mature stands in diameter distribution. Old stands had the greatest frequency of logs ranging in diameter classes from 13 to 29 cm (Figure II-1c).

Frequencies of logs in decay classes differed among forest ages (Figure II-2). In young stands, frequencies were greatest in decay stages three and four (Figure II-2a). Mature stands exhibited greatest frequencies in advanced stages of decay (Figure II-2b). Old stands exhibited a relatively even distribution of logs among all decay stages (Figure II-2c).

Substrate diversity was greatest in old stands (Figure II-3). Old stands had logs available for colonization in decay stages one to seven and in diameter classes of 13 to 45 centimetres. Mature stands were characterized by logs in more advanced decay stages and diameter classes ranging from 13 to 41 centimetres (Figure II-3). Young stands had a wider range of decay stages than mature stands (three to seven), but had a narrower range of log diameter classes (13 to 37; Figure II-3).

Nonvascular Species and Stand Age

Alpha diversity was highly variable among sites within ages (Figure II-4). Young stands had the greatest variation among sites with species richness ranging from zero to 21. Among the 24 sites in mature stands, three to 20 species were found. Old sites had species numbers ranging from five to 19 (Figure II-4; see Appendix for a list of species and abundances).

Gamma diversity was highest in old stands, followed by young stands, then mature stands (Table II-1). A total of 96 species were identified. Of these, 33 were mosses, 32 were lichens, 24 were fungi, and 7 were species of liverworts (Table II-1). The high number of species in old stands was accounted for by mosses, fungi, and to a lesser extent, liverworts. Young stands had more lichens than any other taxonomic group, while mature and old stands were highest in mosses (Table II-1). Using the Shannon Index of diversity, nonvascular species exhibited greatest diversity in young stands, followed by old stands, followed by mature stands. Young stands had the most even distribution of species, followed by mature stands, then old stands (Table II-1). Of the 96 species, 28 were found in all age classes. Ten, 11, and 28 species were exclusive to young, mature, and old stands, respectively.

The number of rare species (i.e., those with low abundance values) greatly outnumbered the number of common species (i.e., those with high abundance values) for all stand ages (Figure II-5). Species frequency, when plotted against species abundance (number of occurrences) , showed old stands had the greatest number of nonvascular species with low abundances, followed by young stands, then mature stands (Figure II-5).

Nonvascular Species and Decay Stage

Species richness increased with decay stage, until stage six, then richness slightly decreased (Figure II-6). The number of species added to the successional sequence as the stands increased in age are presented in Figure II-6. In later decay stages (five to seven), Mature stands contributed a large portion of species that were not detected in young stands. Old stands contributed a large component of previously unsampled species throughout all decay stages.

When species were placed in ecological groups, some differences emerged among decay stages. Epiphytic species had no significant changes in frequency across decay stages (Figure II-7). Epixylic species did not appear until decay stage two, where they were in low frequencies. Epixylics increased with decay, leveled off in stages four to six, then decreased in decay stage seven (Figure II-7). Terricolous species increased with decay stage (Figure II-7).

Richness of species across decay classes was examined by taxonomic units of liverworts, lichens, and mosses (Figure II-8). Mosses were the taxonomic group that contributed most to species richness, followed closely by lichens, throughout all stages of decay, with the exception of decay stage six (Figure II-8). Decay stage seven had the greatest numbers of moss species (n = 25), indicating that lichens were responsible for the

decline in overall species richness. Liverworts did not appear until decay stage three, steadily increased to decay stage five, then declined to decay stage seven (Figure II-8).

To examine the relative contributions of each ecological group within a taxonomic unit, both ecological groups and taxonomic units were combined. There were differences within and between taxonomic groups (liverworts, lichens, and mosses) in abundances of epiphytes, epixylics, and terricolous species across the decay stages. Liverworts reflected the same trend as presented in Figure II-8 because all the liverworts found were epixylic (Figure II-9a). Lichens exhibited a relatively stable to slightly increasing trend as epiphytes and terricolous species until decay stage six, then both groups decreased, while epixylic lichens first appeared at decay stage three, increased to decay stages five and six, then decreased (Figure II-9b). Mosses had fewer species as epiphytes than did lichens across all decay stages (Figure II-9c), the frequency of which remained stable. Frequency of mosses as epixylics was also lower across all decay stages than it was for lichens, with the exception of decay stage two (Figure II-9c). Terricolous mosses exhibited an increasing trend similar to terricolous lichens, with terricolous mosses having greater frequencies than terricolous lichens (Figure II-9c). Trends observed in decay stages one and two may be slightly misleading because of the low sample size of logs in these decay stages (18 and 33 logs in stages one and two, respectively) compared to other stages (remaining stages ranged from 128 to 178 logs). Liverworts and lichens contributed most to the frequency of epixylics, particularly in intermediate decay stages, lichens contributed most to the frequency of epiphytes, and mosses contributed most to the frequency of terricolous species, particularly in more advanced stages of decay.

Discriminant Analysis Across Decay

Discriminant analysis indicated that the seven decay stages were significantly separated by the first five of the six canonical functions (Table II-2). Therefore, the seven decay stages have relatively good predictive potential. A total of 16 observation variables were selected for the analyses (Table II-3), a linear combination of which best discriminated between decay stages.

Bark, wood, and herb variables had the greatest discriminatory importance for the first two canonical functions (Table II-3). The first two canonical functions explained 90.6% of the total variance (Table II-3). The first canonical axis represents the direction of greatest variance (63%) between decay stages. Bark, wood, and herbs were the variables with the highest correlation to the first axis (Figure II-10). This axis is particularly useful in discriminating decay stages one and two from the rest of the decay stages, and it discriminates decay stages five to seven from decay stages three and four. The second

canonical axis represents 38% of the variance between decay stages. The same variables influencing axis one most influence axis two, but the direction of correlation differs for wood and herbs (Figure II-10). Similarly, this axis is most useful in discriminating decay stages one and two from decay stages three to seven.

The overall success in classifying samples into the seven decay stages correctly was 53%. There was good group membership in four of the seven decay stages (Table II-4). Three decay stages were considered missclassified. Decay stage one was more similar to stage two than to itself (5 cases as stage one, 11 cases as stage two). Decay stage four was classified as stage three more often than to itself (32 cases as stage four, 53 cases as stage three). Decay stage five was slightly more similar to stage six than to itself (30 cases as stage five, 37 cases as stage six; Table II-4).

To determine whether log diameter affected species richness, the seven decay stages were placed into four groups (A, B, C, and D) based on the discriminant classification results (Table II-4). Group A consisted of decay stages one and two, group B consisted of decay stages three and four, group C consisted of decay stages five and six, and group D consisted of decay stage seven. Within each of the four groups, regression coefficients were calculated, and the slopes of each age class were compared. Of the four groups, analysis of covariance among regression coefficients revealed significant differences only within decay group D ($F = 12.18$; df = 2, 172; Figure II-11). The Tukey test was used to determine which of the age classes within group D differed (Zar 1984). There was no significant difference between slopes of young and old ages, nor between slopes of mature and old ages ($q_{0.05, 172, 3} = 6.45$), however there was a significant difference between the regression coefficients of decay group D logs of young and mature ages. When ages were averaged within the three remaining decay groups (A, B, and C), significant differences were detected ($F = 44.86$; df = 2, 638; Figure II-12). Decay group C was significantly different from decay groups B ($q_{0.05, 638, 3} = 12.30$) and A ($q_{0.05, 638, 3} = 5.97$).

If distinct assemblages of species on each of the seven decay stages are undetectable, there must be a significant intergradation. To examine these assemblages in detail, proportions of species on logs were averaged for each species, then converted to percentages. Some of the relationships of the more common species with decay stages are presented in Figure II-13. Early decay stages contained species that are typical of epiphytic communities on standing trees (Figure II-13). In general, abundance of epiphytes increased in early decay stages, with overall highest abundances occurring at stage three, while frequency also increased to stage three, then fluctuated. Epiphytic mosses such as *Orthotrichum obtusifolium* Brid. and *Pylaisiella polyantha* (Hedw.) Grout

were present in early decay stages. These mosses, along with *Orthotrichum speciosum* Sturm were the three species of moss most commonly found growing on live trees (Crites, unpublished data). *Pylaisiella polyantha* is a moss typically found at the base of aspen trees in the boreal forest of western Canada (Vitt *et al.* 1988). Ground mosses that were also found in early decay stages include *Plagiomnium cuspidatum* (Hedw.) Kop. and *Brachythecium* spp. These species were also found growing on the lower trunk of aspen trees; therefore their presence on these early decay stages may be due to sampling the lower portions of what were previously live trees, rather than these species colonizing from the ground or via germination on the logs. Lichens typical of epiphytic communities, such as, *Phaeophyscia orbicularis* (Necker) Moberg, *Usnea* spp., *Parmelia sulcata* Tayl., and *Cetraria pinastri* (Scop.) S. Gray were found in early decay stages. Some of these species were also found in later decay stages, but usually in lower abundances (Figure II-13).

Cladina mitis (Sandst.) Hustich and *Platygyrium repens* (Brid.) B.S.G. developed on logs of decay stage two. *Cladina mitis*, which typically grows on humus or soil, continued to grow on all the remaining decay stages, having a maximum abundance on decay stage seven. *Cladina mitis* was likely growing on litter and humus that was present on the log surface. *Platygyrium repens* is a typical epixylic moss, associated with decaying logs without bark (Vitt *et al.* 1988), explaining the greatest abundances in decay stages four, five, and six.

At decay stages three and four, many new species had colonized the logs. On decay stage three, six epixylic and one terricolous species were found. Epixylic liverworts such as *Scapania apiculata* Spruce, *Ptilidium pulcherrimum* (Web.) Hampe, and *Jamesoniella autumnalis* (DC.) Steph. were found in highest abundances on intermediate decay stages. *Cladonia coniocraea* (Floerke) Spreng and *Cladonia gracilis* (L.) Willd., typical epixylic lichens, were growing on decay stages three to seven. One typical epixylic moss that is associated with moist decaying logs was *Bryohaplocladium microphyllum* (Hedw.) Broth.. It had its highest abundance (40%) on decay stage three, and its lowest abundance on decay stage seven. *Sanionia uncinata* (Hedw.) Loeske, a ground moss, also began colonizing logs at decay stage three, and was in highest abundance on decay stages five and six.

Once the logs reached decay stage four there were four ground species (all mosses) and three epixylics (all lichens). *Hylocomium splendens* (Hedw.) B.S.G., *Pleurozium schreberi* (Brid.) Mitt., and *Ptilium crista-castrensis* (Hedw.) de Not are all typical ground feather mosses that are abundant in mature spruce forests (Nienstaedt and Zasada 1990). *Hylocomium splendens* was moderately abundant from decay stages four to seven.

Pleurozium schreberi increased with decay stage, with a maximum abundance of 23% at decay stage seven. *Ptilium crista-castrensis* had lowest abundances at decay stages four and seven, and highest abundance at stages five and six. *Dicranum flagellare* Hedw. was also present. *D. flagellare* is associated with both the ground and decaying wood, but it appears to be most commonly found on the ground. Two of the epixylic lichens were of the genus *Peltigera*. *P. elisabethiae* Gyelnik was present from stages four to seven, and had a high cover value average of 34% on decay stage five logs. *P. praetextata* (Sommerf.) Zopf, less abundant than *P. elisabethiae*, was present in moderate abundances from decay stages four to seven. *Cladonia botrytes* (Hag.) Willd. was the third epixylic lichen that first appeared on decay stage four, where it had its highest abundance, decreasing until decay stage six, and being absent from decay stage seven.

Two epixylic and one ground species colonized logs at decay stage five. *Anastrophyllum hellerianum* (Nees) Schust., an epixylic liverwort, was present in moderate abundances on decay stages five and six only. *Eurhynchium pulchellum* (Hedw.) Jenn., a common epixylic moss of the boreal forest, fluctuated in abundance on decay stages five and six, then increased abundance on decay stage seven. The ground lichen *Cladonia bacillaris* Nyl. began colonizing logs at decay stage five, peaked in abundance on decay stage six, then decreased slightly on stage seven.

On decay stages six and seven two ground mosses were present, *Dicranum undulatum* Brid. and *Climacium dendroides* (Hedw.) Web. & Mohr. Both species are associated with mesic habitats, with the former having greatest abundance values on stage six, the latter on stage seven.

Substrate Separated from Stand Age

Where possible, numbers of DWM were equalized across stand ages, within decay classes (Table II-5), and species richness and composition were compared. Decay stages one and two had too few logs in two of the three stand ages for data reduction. Decay stages three and four had too few logs in mature stands; therefore data from young or old stands were removed to allow for equal representation, then the two stand ages were compared (Table II-5). Decay stage seven logs were not included in the comparison of species across stand ages because the communities on these logs were already found to be significantly different based on log diameter (Figure II-11).

Nonvascular species richness, when using the complete dataset, was highest in old stands in all four of the decay stages presented (Figure II-14). With a reduced dataset of equal numbers of logs within each decay stage, old stands were highest in species richness in two of the four decay stages presented (Figure II-15), but were still highest in overall

species richness (n = 50, 45, and 56 in young, mature, and old stands, respectively). With equal log numbers, the number of species exclusive to one stand age only changed for old stands (from n = 28 to n = 21). Nonvascular species richness across decay stages ranged from 14 - 30 species. The number of species shared between two or three ages, depending on the number of age classes compared, ranged from four to 11 species, or from 15 - 55%. Therefore, the stand ages still appear to be quite different with equal numbers of logs within each decay stage.

Pairwise dissimilarity coefficients revealed that all age classes were dissimilar within decay stages (Table II-6). Decay stage seven was the most similar in species composition and abundance between young and mature stands, followed by decay stage two between young and old stands (Table II-6). Species richness and abundance became increasingly similar with decay stage.

Discussion

Downed Woody Material

A successional pattern of DWM was evident. Diameters of DWM in young stands, together with data on diameters of live trees in young stands, provide evidence that these logs were likely from pre- and post-fire origins. During a fire, many trees are killed or injured. Of these, many trees remain standing and become snags while others fall to the forest floor. By the time the stand reached 25 years of age, the majority of these logs had decayed to stage three (Figure II-2a). The remaining logs that are not of pre-fire origin are a result of the self-thinning that occurs in young stands among trees competing for light and space (Harmon *et al.* 1986, Peterson and Peterson 1992). These smaller logs, by 25 years stand age, were at decay stages three and four (Figure II-2a).

Mature stands consisted of relatively healthy trees as evidenced by little input into early DWM decay stages and low frequencies. The logs that were decaying were likely the result of the "pulse" of woody material input after the stand-originating fire, combined with logs that were present before the fire event. These were likely the same cohort of logs that were in decay stages three and four in the young stands. The diameter of the logs leveled out slightly (Figure II-1b), indicating that between the young and mature ages, there were inputs of DWM onto the forest floor from a wider range of tree ages. These are likely the result of a combination of factors, such as insect outbreaks, wind, disease, and mammal damage, but due mainly to self-thinning that continued until the trees had become established.

As succession proceeds, the rate of input and the size of pieces added to the forest floor increases (Harmon *et al.* 1986, Lesica *et al.* 1991). Old stands had a more variable distribution of decay and size of DWM. Both the decay stages and diameters leveled out and frequency once again increased (Figures II-1c, II-2c). This is thought to be the result of fungal invasion and wind-related mortality (Basham 1958, Harmon *et al.* 1986). Older, unhealthy trees are killed by fungi and insects, but may remain standing as snags (Basham 1958). Eventually, wind or lack of support structures causes them to fall to the forest floor where they become part of the DWM pool. The trees that die are usually large (resulting in high volumes), producing a large gap in the forest canopy. A combination of light penetrating the forest floor through such gaps and the loss of apical dominance leads to aspen regeneration (Peterson and Peterson 1992). These processes occur throughout the stand, creating a stand that has multiple tree ages and a multi-layered canopy. Of the trees that colonize forest gaps, some will become a part of the DWM pool due to factors such as wind, damage caused by falling trees, insects, and disease (Peterson and Peterson 1992). The chance of fungal attack in old stands is high due to the large number of fungal species present in old and decaying trees (Basham 1958), increasing the relative number of spores compared to younger stands. The above factors combined give rise to a continuous input of woody material in old stands, resulting in a broad range of decay stages (Figure II-2c), a broad range of diameters, and high frequencies (due to the deaths of both young and old trees; Figure II-1c).

Rate of DWM decay can be affected by many factors including the structural quality of the tree when it fell, diameter, height above ground, moisture, species of tree, climate, and colonizing organisms (Swift 1977, Harmon *et al.* 1986, Söderström 1988b, Harmon 1993). The substrate of decaying logs is dynamic. Factors such as bark loss, crevice formation, pieces lost, decomposition, and damage by animals or falling trees, can make the surface rougher, and thereby facilitate colonization. A smooth surface may be more difficult for a propagule to become established on (Söderström 1988b). The rate at which surface changes and rot proceeds are dependent on the local environment. This makes it difficult to find distinct characteristics of a particular decay stage, including species assemblages. Some logs may decay at a faster rate due to these factors, which may then lead to a different assemblage of species than other logs of the same decay stage.

Nonvascular Species and Stand Age

Alpha diversity, as measured by the range in species richness within each age class, had the highest variability in young stands. This high variability can be explained by the patchiness of substrate distributions. Of the four young stands sampled, two stands

had very little downed woody material, while two stands had high amounts of downed woody material. The differences between the downed woody material distributions among young stands is a reflection of the severity of the stand-initiating fires. One site had no nonvascular plant species present on downed logs. This is a result of little woody material being present in this site.

Species richness, as measured by gamma diversity, and the number of rare species were greatest in old stands, but species diversity and evenness as measured by the Shannon Index were highest in young stands (Table II-1). In all stand ages there were many more rare species than common ones (Figure II-5). The nonvascular plant species that were present in low abundances occurred most frequently in old stands (Figure II-5). The species in this group were mostly fungi. This could be reflective of a more humid microclimate in old stands. Similarly, Lesica *et al.* (1991) found more species of rare trunk epiphytes, and the highest species richness, in old stands. Conservative management of old aspen stands is essential to maintain this rare fungal component (see Appendix).

The high diversity and evenness values of young stands may be explained by fewer rare species found in young stands than in old stands, and the most abundant species in young stands were lower in abundance than the most abundant species in old stands (Figure II-5). Lower extremes in abundance values, when factored into a diversity index, will lead to a higher diversity value with more species evenly spread out. Similar patterns of species abundance in bryophytes were found by Vitt (1991). Tracheophytes, however, exhibit a reverse "J" curve instead of the negative exponential curve found with bryophytes (Kent and Coker 1992). The negative exponential curve illustrates rarity in mosses (Figure II-5). Most mosses occur disjunctively or are continuously widespread (Vitt 1991), however in this dataset and that of Vitt's most species were locally rare. Vitt (1991) concluded that this was due to a combination of the species having specialized habitat requirements and the habitats being spatially or temporally rare. My results agree with these, as the habitats measured in this study (DWM) were both spatially and temporally rare, depending on age class.

The significant difference in regression coefficients between young and mature stands of decay group seven indicates that the species in the two forest age classes changed at different rates, or had different rates of colonization, which may be related to the spatial scales of log distribution. That is, because young and mature stands differ in the rate of species change on group D logs, we can not accurately compare nonvascular communities between these ages because growth and colonization rates differ.

In plant communities such as these, species are highly dependent on substrate and microclimate (Muhle and LeBlanc 1975, Lee and La Roi 1979a, Söderström 1988a, Lesica

et al. 1991). For dispersal to succeed, substrates must be available. Old stands provided a greater diversity of substrates than young or mature stands (Figure II-3), and perhaps the microclimatic conditions were optimal for species growth and reproduction. It is species numbers and composition that are of concern in such communities because if there are rare occurrences, the community is then providing a source habitat from which colonization of surrounding areas can occur.

Most studies tend to discount rare occurrences (e.g., Söderström 1988b). Species diversity measures can be misleading and have caused much controversy among ecologists (Kent and Coker 1992). Diversity indices take into account species numbers and relative abundances; in this regard, rare species that are present in low abundances are de-emphasized. Also, many researchers remove rare species from more detailed analyses. For example, Söderström (1988b) used the 25 most common species out of 75 species found for more detailed analyses, with 40 of the 75 having at least five occurrences. Rationale for removing rare species may be justified in some studies. In nonvascular plant communities such as the one I am studying, I believe that rare species are as important as common species because we need to be concerned with species conservation in threatened communities. Areas with unique species assemblages need to be identified and protected (Gustafsson *et al.* 1992a). In Alberta, there is nothing analogous to Sweden's red list of endangered and threatened species. Rare species or unique species assemblages in such communities can serve as indicators, or simply by their occurrence, can provide important information about that community distinguishing it from other communities where these plant assemblages are not found. With the high number of species found to be exclusive to old stands (n = 28), these stands require special management to ensure the survival of these species. We should be concerned about rare species, and seek to discover why they are occurring where they do, what are the processes that lead to their occurrence, in order to ensure their survival in a boreal forest landscape managed for wood fiber.

Nonvascular Species and Decay Stage

As decay proceeded, species richness increased up to decay stage 6 (Figure II-6). By examining the changes in species and ecological groups with decay stages, we can describe a successional pathway. There are two temporal factors that explain the pattern in Figure II-6. Stand age and decay stage of DWM both contribute to species richness. Many nonvascular plant species are slow-growing (Larson 1984). It takes time for an ecosystem to have a suitable combination of factors for optimal growth of nonvascular species. It also takes time for species to colonize particular habitats. It takes time for DWM of decay stages five, six, and seven to be colonized by species, but these decay

stages may also be unique in the chemical and physical composition of their substrates and their specific microclimates, such as moisture regimes and surface texture. Many species may only successfully colonize a particular substrate when all biophysical conditions are suitable at exactly the same time, which is likely rare. Such conditions include dispersal ability, wind speed, surrounding substrates (i.e., decay stages and densities), moisture levels of the substrates and the surrounding stand, species colonizing adjacent substrates, and conditions suitable for germination (i.e., light, water, nutrients). Many of these factors co-vary. The likelihood of all these factors being suitable for nonvascular plant colonization is greater in older aspen forests, as evidenced by our species distribution data. The many factors that are responsible for creating such an ecosystem would be difficult, if not impossible, to recreate by artificial means.

The ecological groups provided an indication of the successional pattern on the logs. It is expected for epiphytes to occur in higher frequencies on logs in early stages of decay, as these species would be already present on the tree when it was alive. The epiphytes would then be replaced by epixylics, which are expected to have highest frequencies in intermediate stages of decay, once they have had time to become established. Terricolous species would be expected to then increase as decay proceeded and as the log was decomposing into the ground. The colonization of these species from the ground to the upper surface of a log densely covered by a combination of litter and other species, would be relatively unimpeded. My results show a similar pattern. Epiphytes, however, did not exhibit a continual decline with increasing decay (Figure II-7). Epiphytes increased in abundance (i.e., area covered by individual species) until decay stage three, coupled with an increase in frequency (i.e., number of species). This is likely because of the low sample size of logs in decay stages one and two (18 and 33 logs, respectively). More logs would have to be sampled to reflect the true epiphytic distribution found on live trees. It should be noted, however, that epiphytes on aspen trees in temperate forests are relatively sparse (Crites, unpublished data) compared to epiphytes in old-growth conifer forests (see Pike *et al.* 1975, Lesica *et al.* 1991, McCune 1993). Epixylics and ground species will completely colonize the available substrate until no wood or humus is visible.

Epixylic species exhibited a trend similar to the expected pattern. Epixylic species did not find the logs suitable for colonization until decay stage two, when two species were able to colonize (Figure II-7). Conditions were optimal at decay stages four to six with 10, 11, and 10 species, respectively, found growing on DWM. These decay stages consist of logs with little to no bark, making them unsuitable for most epiphytes. There is little known about the effect of decomposition substances on bryophytes and lichens. It

has been suggested that the decomposition products may control the sequence of bryophytes on some logs (Muhle and LeBlanc 1975). Terricolous species continually increased to a maximum of 32 species at decay stage seven (Figure II-7). The presence of terricolous species in early decay stages can be explained by the sampling method used. Many terricolous species were found growing on live tree bases. That is, they were growing on the ground or decomposing wood or humus that was surrounding a tree, and this would put them in a position to colonize the tree base. These species are unable to survive past the first few centimetres of a tree base, hence they are restricted here due to microclimate. Once a tree falls to the forest floor and becomes part of the DWM pool, ground mosses remain attached to the base of the tree. With the sampling method used, the portion of the log that intersected the transect was sampled, regardless of what portion of the previously standing tree it was. Therefore many tree bases were likely sampled, explaining the existence of ground species in early decay stages. As decay continued, the wood decomposed to the point of humus, providing moisture and nutrient-rich substrates that ground species thrive in.

Liverworts had a maximum number of five species on decay stage five (Figure II-8), and six species were found in old stands, compared to four species found in young and three species found in mature stands (Table II-1). Both Lesica *et al.* (1991) and Söderström (1988a) found liverworts to be the taxonomic group most sensitive to microclimate and substrate, and most likely to be threatened in managed stands. This is likely because most liverworts are epixylic and suitable epixylic habitat occurs only in intermediate stages of decay (Söderström 1988a). It has been suggested that logs in intermediate stages of decay may be scarce in managed stands (Söderström 1988a), and that epixylic liverworts, in particular, may be threatened by intensive forest management (Muhle and LeBlanc 1975, Lesica *et al.* 1991). Managed stands will not have the same microclimate found in old stands, which these liverwort species seem to prefer. These sensitive species need to be considered in future forest management plans.

Discriminant Analysis of Decay Stages

The discriminant analysis indicated there were predictable assemblages of nonvascular species on four of seven decay stages. That is not to say that the remaining decay stages were not used by the species, but there were not distinct and predictable groups inhabiting decay stages one, four, and five. The observed variables that did serve to discriminate the first two canonical axes, bark, wood, and herbs, broadly define the difference between early and later decay stages. Early decay stages were typically uncolonized; therefore bark and wood were sampled most, later decay stages experienced

increased colonization by herbs. The fact that the overall classification success of the canonical model was relatively low (53%), indicates that these species distributions and abundances were variable, and not highly predictable, however other factors serve as significant predictors. None of the three variables that largely control the first two canonical axes, is a nonvascular plant, therefore the variance in bark, wood, and herbs predicts a significant amount of variance in nonvascular species. The factors controlling the species distributions are likely complex, and difficult to identify in a field study. Dispersal and substrate availability need to be closely examined. For species to survive on a spatially patchy and temporary substrate, suitable substrates need to be in close proximity, and dispersal needs to be efficient. Vegetative dispersal alone will not be sufficient to ensure the survival of a population in an aspen forest.

There was a successional trend in the distributions of species. Assemblages were being succeeded and replaced, or the abundances were decreasing while others were increasing, throughout all decay stages. The more common species of epiphytes decreased with increasing decay. Epixylics colonized intermediate stages, particularly the sensitive liverwort group. Terricolous species increased with increasing decay as the log became moister and covered by litter, then soil, resembling the ground by decay stage seven. Portions of logs in advanced stages of decay may not be completely colonized by epixylic or ground mosses. Such areas may still support the epiphytes that were growing on it when the tree fell. Bark can fall off in random patches and there may be some small patches of bark remaining on logs in advanced stages of decay. These epiphytic lichens may have been located in a position on the log that had an unfavorable microclimate or was inaccessible to dispersing spores. Another point of consideration is the low sample size of logs in early decay stages. There were only 18 and 33 logs sampled in decay stages one and two, respectively. Decay stages three to seven had log numbers ranging from 126 to 178. The expected pattern is one of overall gradual decline in epiphytes, but this was not demonstrated. Söderström (1988b) concluded that epixylics colonize early after the tree has fallen down and increase in both frequency and abundance until a peak is reached in early or mid decay stages. In mid decay stages logs are usually dominated by epixylics. My results support Söderström's (1988b) findings.

One conclusion, based on the discriminant analysis results, is that there were only four useful decay stages based on species groups, hence habitat. I believe this is not the case, based on the descending pattern in Figure II-13. What this actually indicates is that species groupings are not predictable, but every decay stage is used by a host of species with high intergradation. Perhaps all these stages were essential for the observed species patterns to occur. If particular decay stages are absent, spores may not be able to

germinate on the substrate because another species may be occupying that site, or other conditions of the DWM are not suitable. My results are similar Söderström's (1989). He found that of 18 species found on downed logs, most of them were found throughout the entire range of measured decay stages. The best conclusion is that once we know the distribution of DWM and nonvascular species in natural systems, a reconstruction of appropriate substrate and microclimate will produce the same species. However, we do not know, and probably never will, the factors controlling the species distributions other than substrate, given that fine-scale microclimatic factors are difficult to measure, as are reproductive capabilities. The host of microclimatic variables that control species distributions are difficult to measure, but other studies have shown that time is an important element. It takes time for an ecosystem to develop suitable conditions conducive to nonvascular plant colonization. Important variables identified in other studies are stand age, continuity of forest attributes (time since disturbance), canopy cover, and abundance of downed logs. Most can be reconstructed except for time since disturbance.

Substrate Separated from Stand Age

When log numbers were equalized between stand ages, species richness decreased in all stand ages. Old stands, however, remained the most species rich (n = 56), and had the greatest number of exclusive species (n = 21). Of the 50, 45, and 56 species found in young, mature, and old stands, respectively, with equal numbers of logs, 21 species were found in all three ages.

The CRD indices indicated that all pairs of decay stages were dissimilar. The CRD dissimilarity index puts greater importance on the relative proportions of species on logs and less importance on their absolute quantities (Ludwig and Reynolds 1988). Species richness within decay stages across stand ages would be very misleading without also examining composition and abundance. None of the decay stages had dissimilarity indices that were close to 0, which would have indicated the decay stages were identical between two stand ages based on species composition and abundance. The number of shared species across decay stages within stand age ranged from four to 11, or 15 - 55%, which is low considering the number of species ranged from 14 - 30. This relatively low value of shared species, when combined with the dissimilarity indices results, indicates that the stand ages differed in species composition and abundance. That is, a log of a particular decay stage in a young stand was different from a log of the same decay stage in a mature stand, which also differed from a log of the same decay stage in an old stand.

These results indicate that nonvascular plant species do not depend only on

structural attributes such as decay stages and their distributions. Stand age, or time since disturbance, is also an important factor to nonvascular plant composition and abundance. Each stand age had a unique component of nonvascular species composition and abundance. If time was not an important element to nonvascular communities, we would expect there to be many more shared species between age classes and lower dissimilarity coefficients, when equal numbers of logs are sampled in each age. These results are unique because other studies have not attempted to separate the importance of structural attributes, such as substrate, from age of the stand.

Old aspen stands of this study provided a greater diversity of substrates for nonvascular plant colonization. The substrates were valuable as evidenced by the greater species richness in old stands and greater number of exclusive species. This study also demonstrated that there are unique species assemblages on some of the DWM, but all of the decay stages identified were used by some species. Old stands provided the greatest diversity of substrates; therefore these stands have the potential to be colonized by the greatest number of species. Rarity in nonvascular species is dependent on habitat occurrence (Vitt 1991). Species persistence depends on effective colonization and establishment rates, together with high extinction rates (caused by the temporary nature of the habitat)(Vitt 1991). The greater the diversity of substrates available for colonization, and the more abundant the substrate, the greater the chance of successful dispersal. These conditions are met in old stands of aspen more so than in mature stands. Young stands have abundant substrates, but they are not diverse. That is, in young stands most of the logs are of small diameters or are in early decay stages. Mature stands have a greater substrate diversity than young stands, but DWM is of low densities. Old stands fulfill both criteria, having the highest substrate diversity (range of diameter and decay) and high substrate abundances (Figure II-3). When substrate was separated from stand age, all ages appeared to have unique assemblages of nonvascular species, with few species being shared across decay stages within stand ages. Therefore, nonvascular plant communities depend on substrate and stand age. It is within stand ages that microclimatic conditions may be unique resulting in unique species assemblages. It would be valuable to examine microclimate in more detail, as well as ecological requirements of unique species.

Table II-1. Gamma diversity and Shannon Index for nonvascular species in young, mature, and old aspen mixedwood stands in northeastern Alberta.

	Young	Mature	Old	Total
Gamma diversity	54	49	71	96
mosses	20	23	25	33
lichens	23	20	23	32
liverworts	4	3	6	7
fungi	7	3	17	24
Shannon Index	2.92	2.51	2.63	
Evenness	0.74	0.63	0.62	

Table II-2. Discriminant analysis results of chi-square and significant values produced for the six canonical functions.

After Fcn	Chi-square	df	P-value
0	2202.36	96	0.0000
1	1051.89	75	0.0000
2	346.91	56	0.0000
3	183.73	39	0.0000
4	43.20	24	0.01
5	16.87	11	0.25

Table II-3. Discriminatory importance of the observation variables shown by the within group correlation coefficients between variables and first two canonical functions. For each function, the three variables with the highest correlation coefficients are in bold. The second row consists of percent variance explained by the respective canonical functions.

Observation Variables	Function 1	Function 2
Variance Explained	62.8%	27.8%
Brachythecium spp.	0.02	-0.10
Bryohaplocladium microphyllum	-0.07	-0.13
Bark	**0.97**	**0.56**
Wood	**0.92**	**-0.63**
Litter	-0.07	0.13
Herbs	**-0.38**	**0.46**
Pylaisiella polyantha	0.19	-0.09
Cladonia coniocraea	-0.03	0.01
Xanthoria polycarpa	0.07	0.12
Physcia adscendens	0.17	0.33
Usnea spp.	0.19	0.19
Phellinus tremullae	0.06	0.13
Physarum sp.	-0.08	-0.20
Trametes hirsuta	0.07	0.12
Bjerkandera adjusta	-0.07	-0.30
white crustose lichen*	-0.11	-0.24

*not identified at time of printing

Table II-4. Discriminant classification results of predicted group membership with seven decay stages as groups.

Group (decay)	No. of Cases	Predicted Group Membership 1	2	3	4	5	6	7
1	18	5 **27.8%**	11	1	0	0	1	0
2	33	1	28 **4.8%**	4	0	0	0	0
3	173	0	13	142 **82.1%**	12	1	3	2
4	126	0	3	53	32 **25.4%**	13	20	5
5	125	0	2	15	16	30 **24.0%**	37	25
6	173	0	2	6	6	16	76 **43.9%**	67
7	178	0	0	0	0	2	48	128 **71.9%**

Table II-5. Number of logs in young, mature, and old aspen mixedwood stands across decay stages. Bottom row is the sample size of logs that each decay stage was reduced to for comparisons across age classes.

Age	1	2	3	4	5	6	7
Young	1	3	128	80	45	45	32
Mature	3	2	2	6	22	54	87
Old	14	14	43	40	58	74	60
Reduced	NA*	NA*	43†	40†	22	45	NA‡

*omitted due to too few logs in young and mature stands.

†Mature stands were omitted due to low sample sizes of logs.

‡omitted because a significant difference was previously found across ages

Table II-6. Dissimilarity coefficients calculated using chord distance (Orloci 1978) of decay stages 1-7 across young, mature, and old aspen mixedwood stands. A value of 1.00 indicates decay stages are dissimilar based on species composition and abundance, while a value of 0 indicates decay stages are identical.

Comparison	1	2	3	4	5	6	7
Y & M	1.00	1.00	1.00	0.84	0.62	0.58	0.30
Y & O	0.92	0.41	0.68	0.74	0.45	0.50	0.61
M & O	1.00	1.00	0.98	0.89	0.56	0.53	0.61

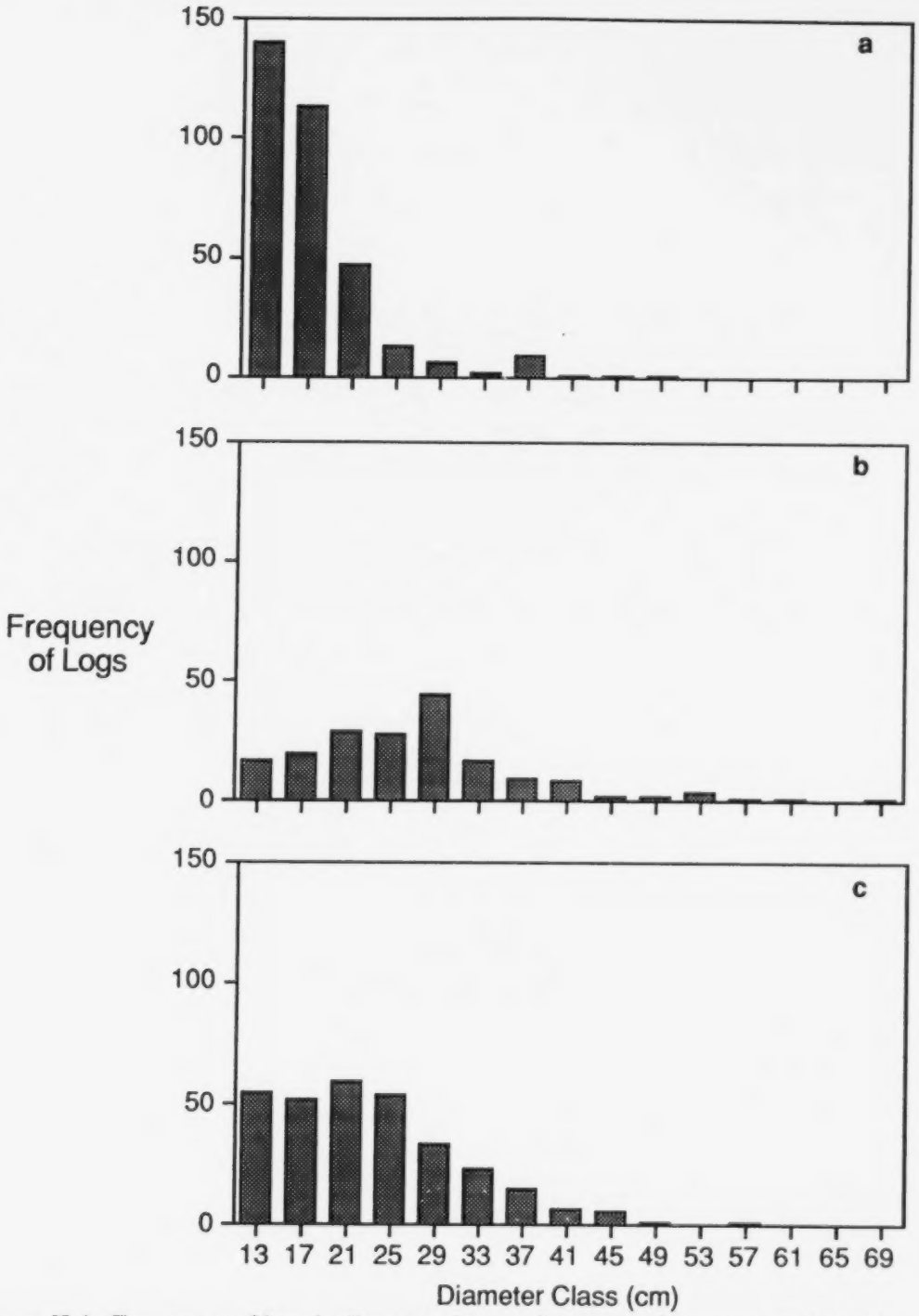

Figure II-1. Frequency of logs in diameter classes of a) young, b) mature, and c) old aspen mixedwood stands in northeastern Alberta.

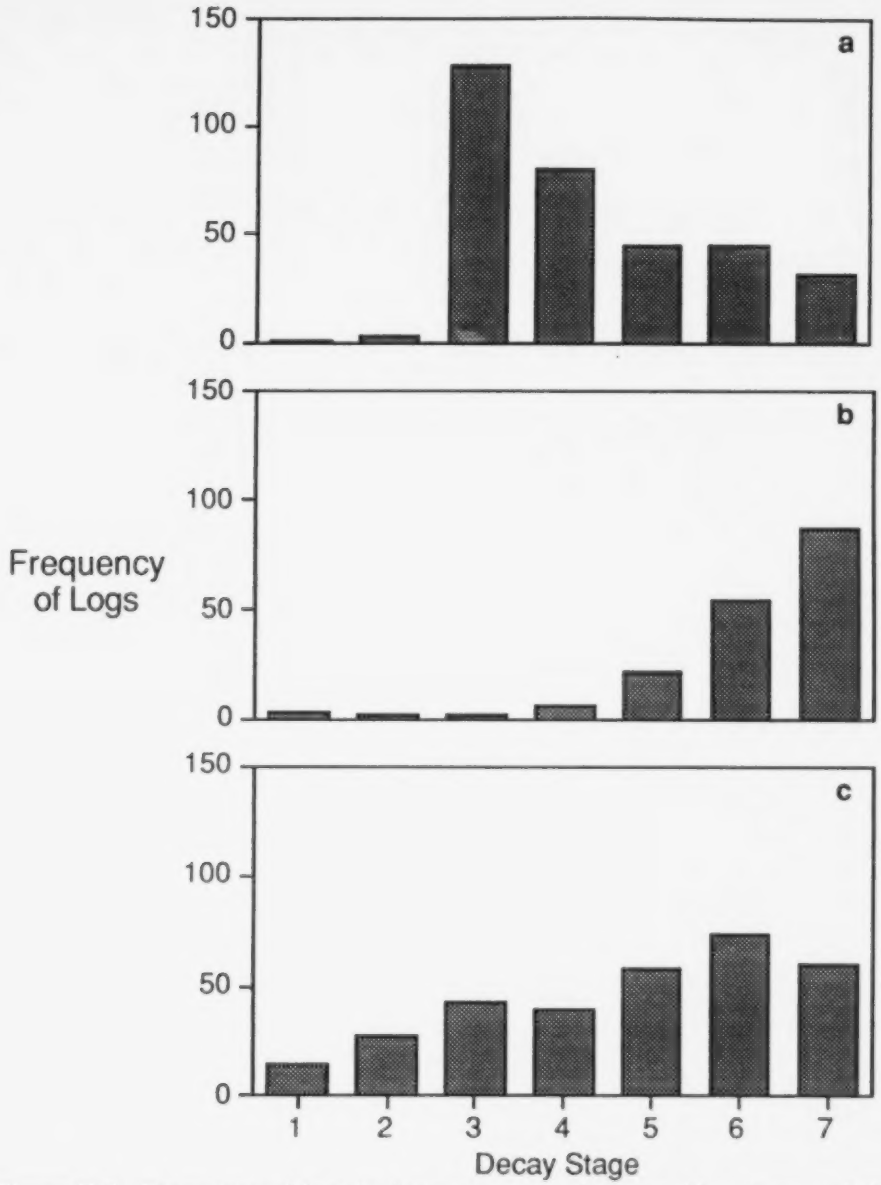

Figure II-2. Frequency of logs in decay stages in a) young, b) mature, and c) old aspen mixedwood stands in Alberta. Decay stage one refers to freshly fallen trees, decay stage seven refers to logs almost completely decomposed.

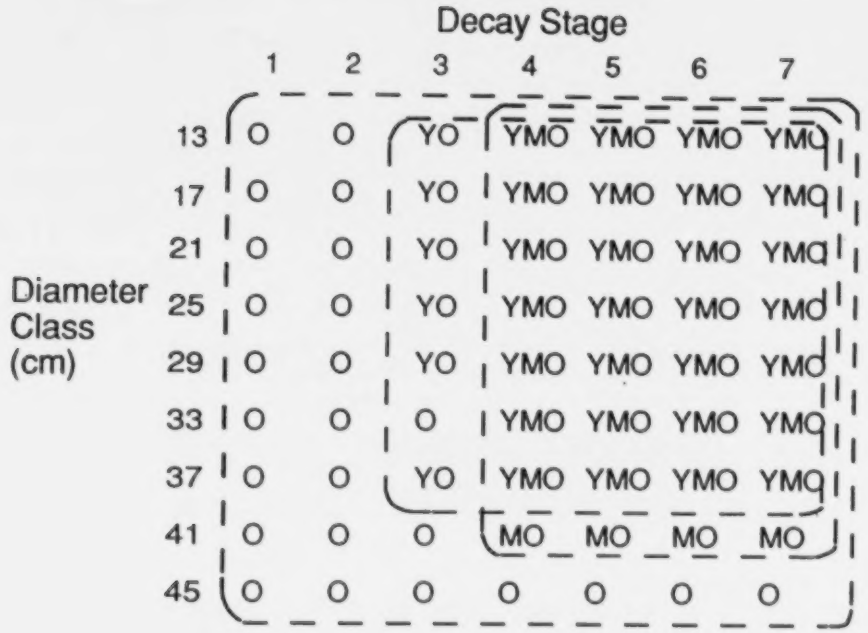
Decay Stage
1 2 3 4 5 6 7
Diameter Class (cm)
13 O O YO YMO YMO YMO YMO
17 O O YO YMO YMO YMO YMO
21 O O YO YMO YMO YMO YMO
25 O O YO YMO YMO YMO YMO
29 O O YO YMO YMO YMO YMO
33 O O O YMO YMO YMO YMO
37 O O YO YMO YMO YMO YMO
41 O O O MO MO MO MO
45 O O O O O O O

Figure II-3. Age classes of Young (Y), Mature (M), and Old (O) aspen mixedwood stands placed in diameter classes and decay stages to represent the diversity of substrates available in the different age classes. Dashed lines indicate the limits of the available substrates for the three respective age classes.

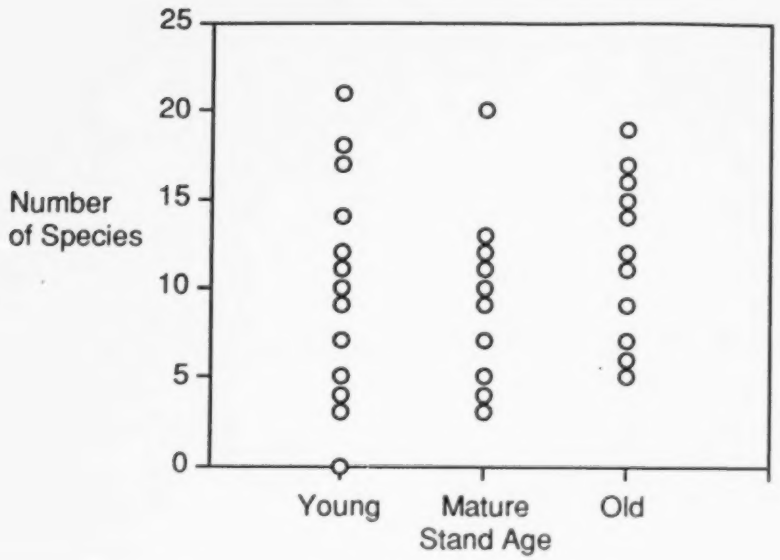

Figure II-4. Alpha diversity within young, mature, and old aspen mixedwood stands. Data points represent the number of species found within each site. Twenty-four sites were sampled within each age.

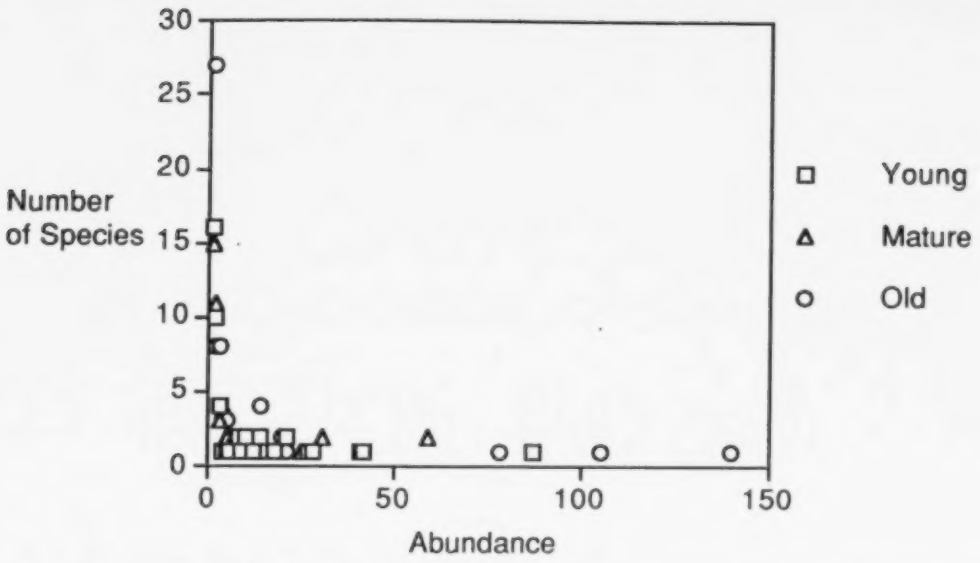

Figure II-5. Patterns of species abundance plotted as number of species against species abundance (number of occurrences) in young, mature, and old aspen mixedwood stands.

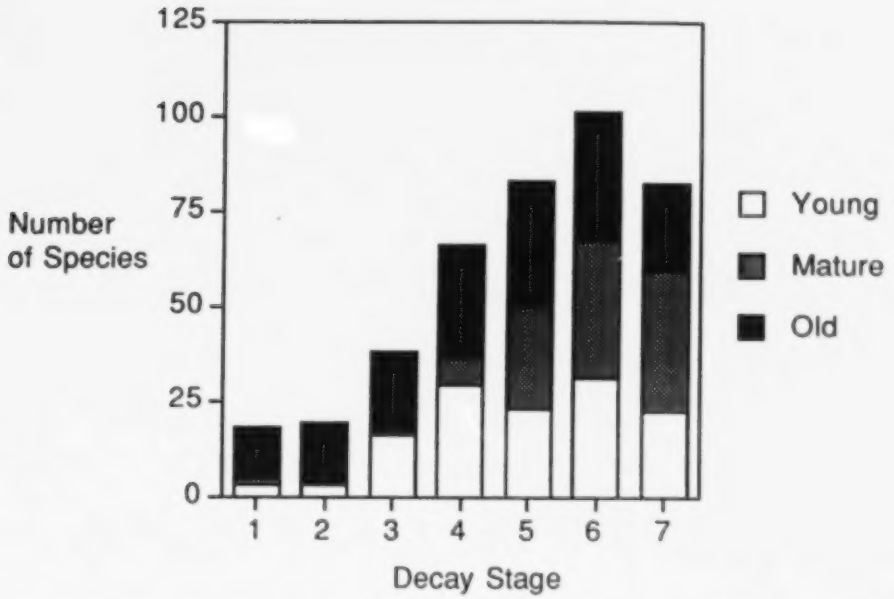

Figure II-6. Species richness in three age classes of aspen mixedwood stands by decay stage. Portions of the bars indicate how many species were added with increasing stand age.

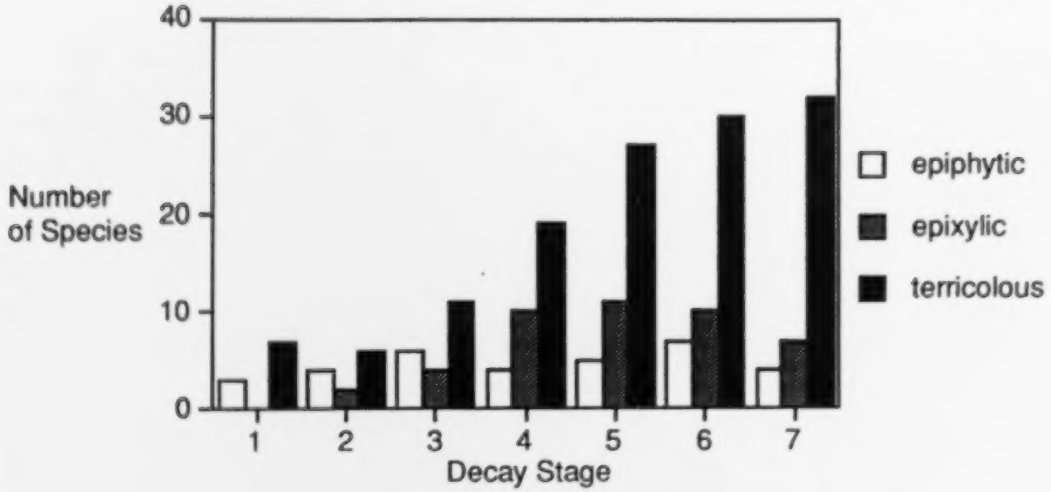

Figure II-7. Number of nonvascular plant species across decay stages. Species are placed into ecological groups of epiphytes, epixylics, and terricolous species.

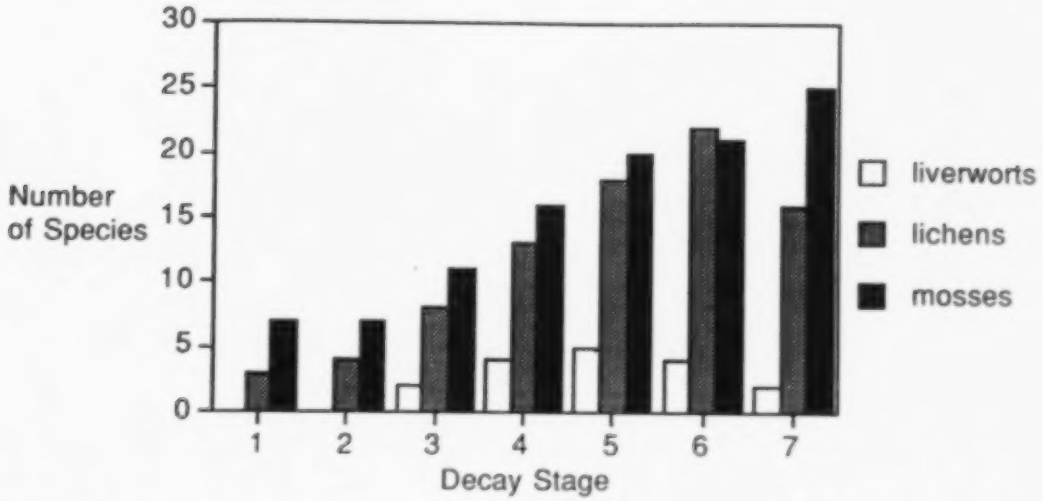

Figure II-8. Number of nonvascular plant species across decay stages. Species are placed into taxonomic groups of liverworts, lichens, and mosses.

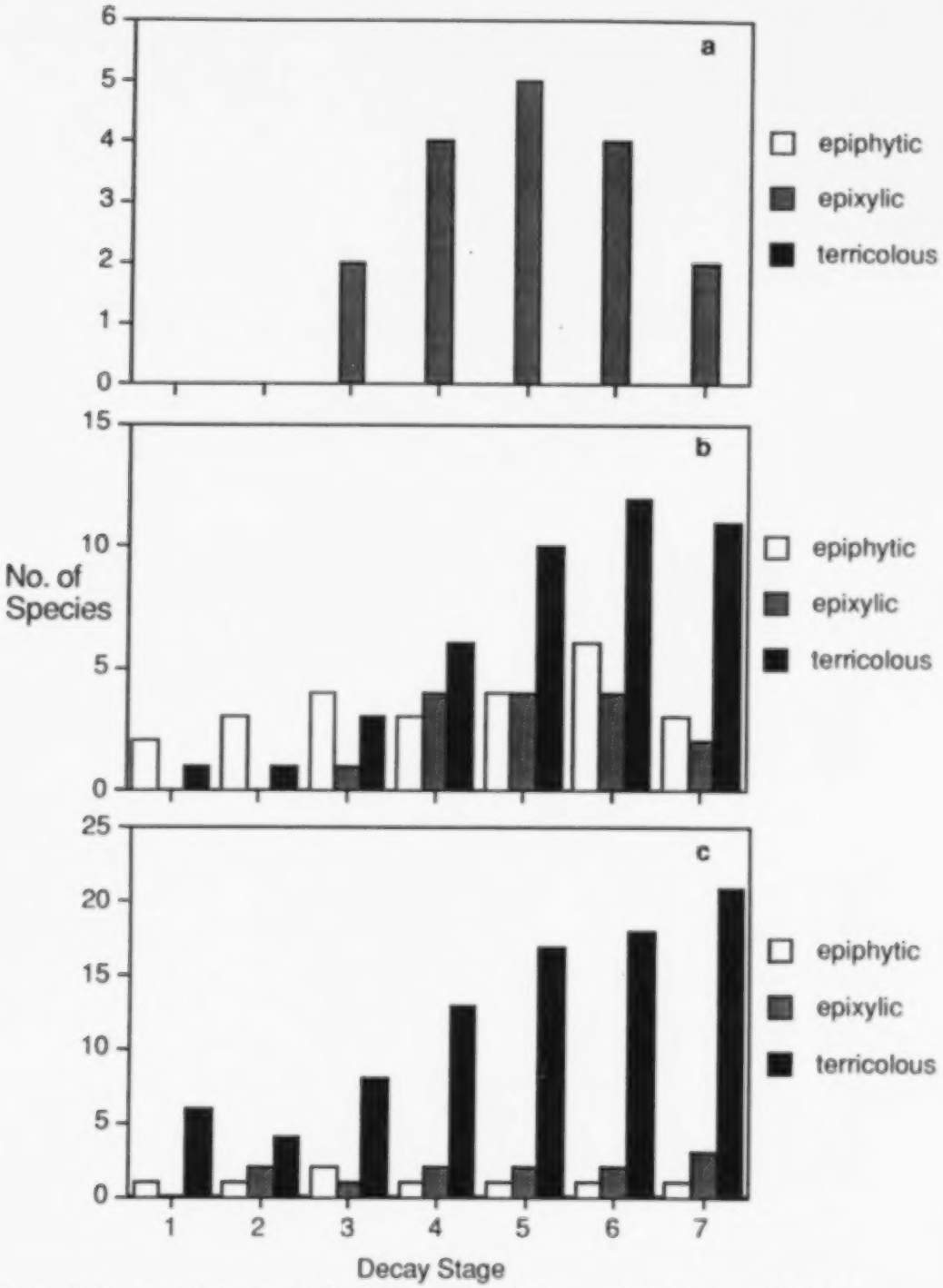

Figure II-9. Taxonomic units of a) liverworts, b) lichens, and c) mosses divided into ecological groups across decay stages.

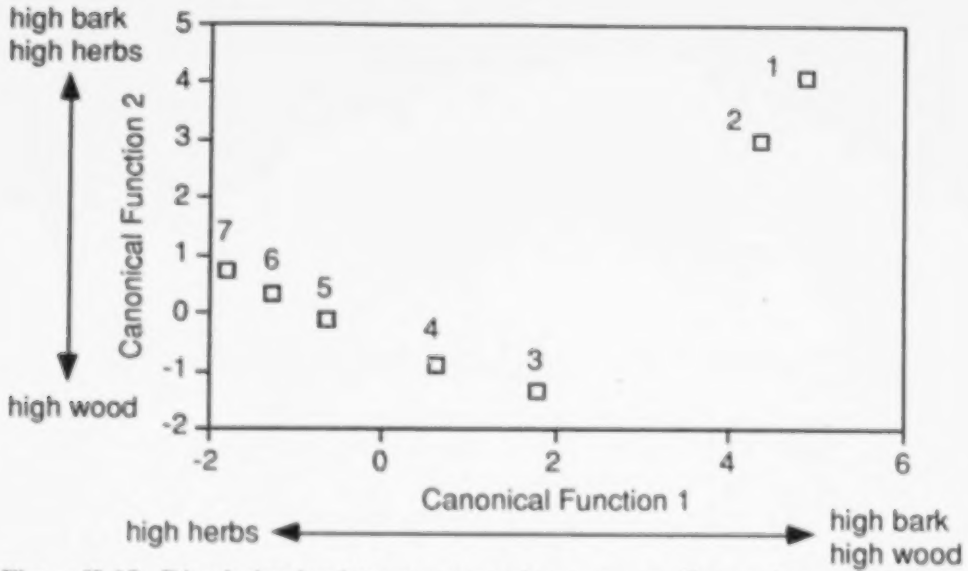

Figure II-10. Discrimination between seven decay stages. Data points represent the centroid for each decay group on the first two canonical axes. Decay stage one represents a freshly fallen tree, decay stage seven represents a log almost completely decomposed.

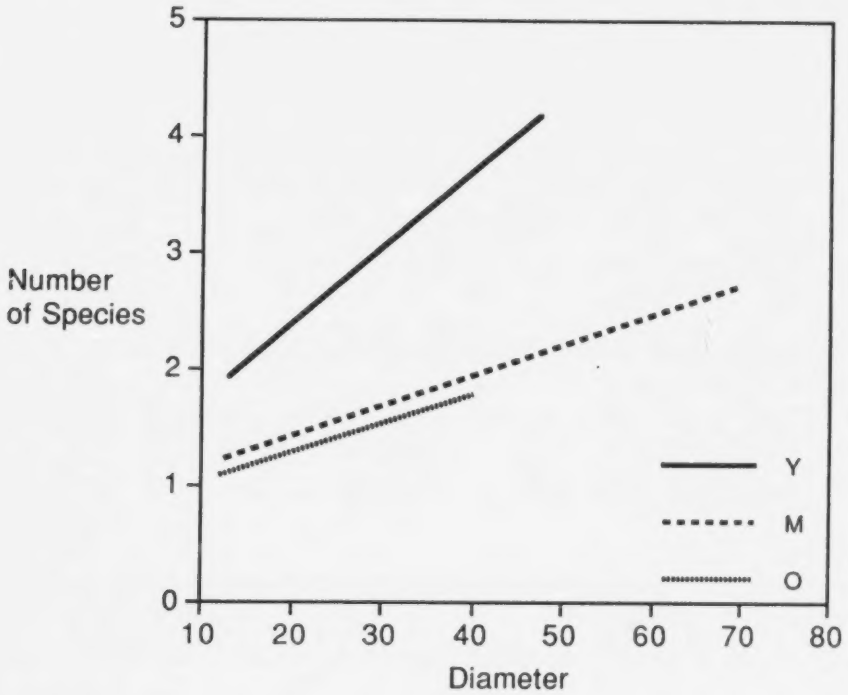

Figure II-11. Regression lines of number of species against log diameter for logs of decay group D in young (Y), mature (M), and old (O) aspen mixedwood stands in Alberta.

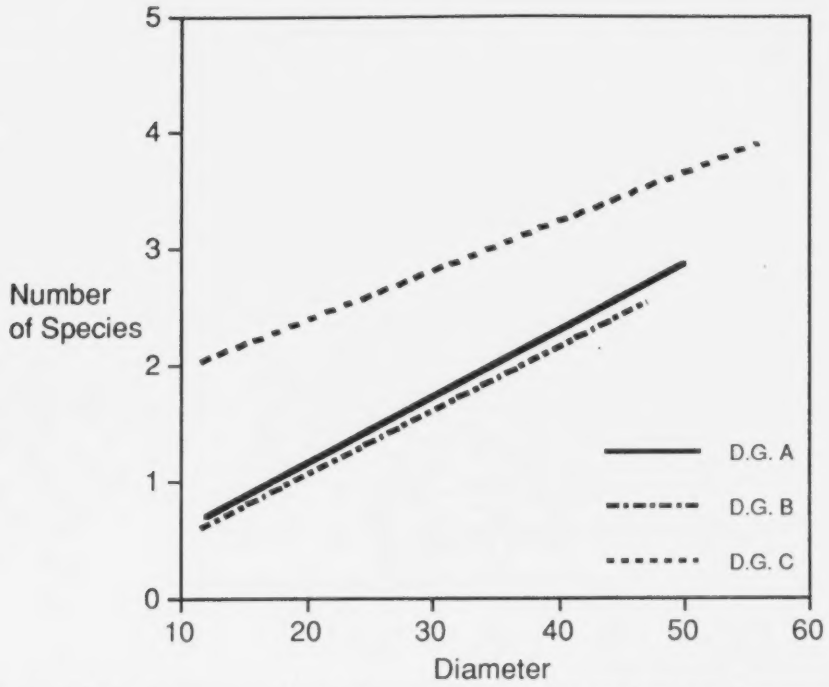

Figure II-12. Regression lines of number of species against log diameter with age classes averaged within decay groups (D.G.) A, B, and C.

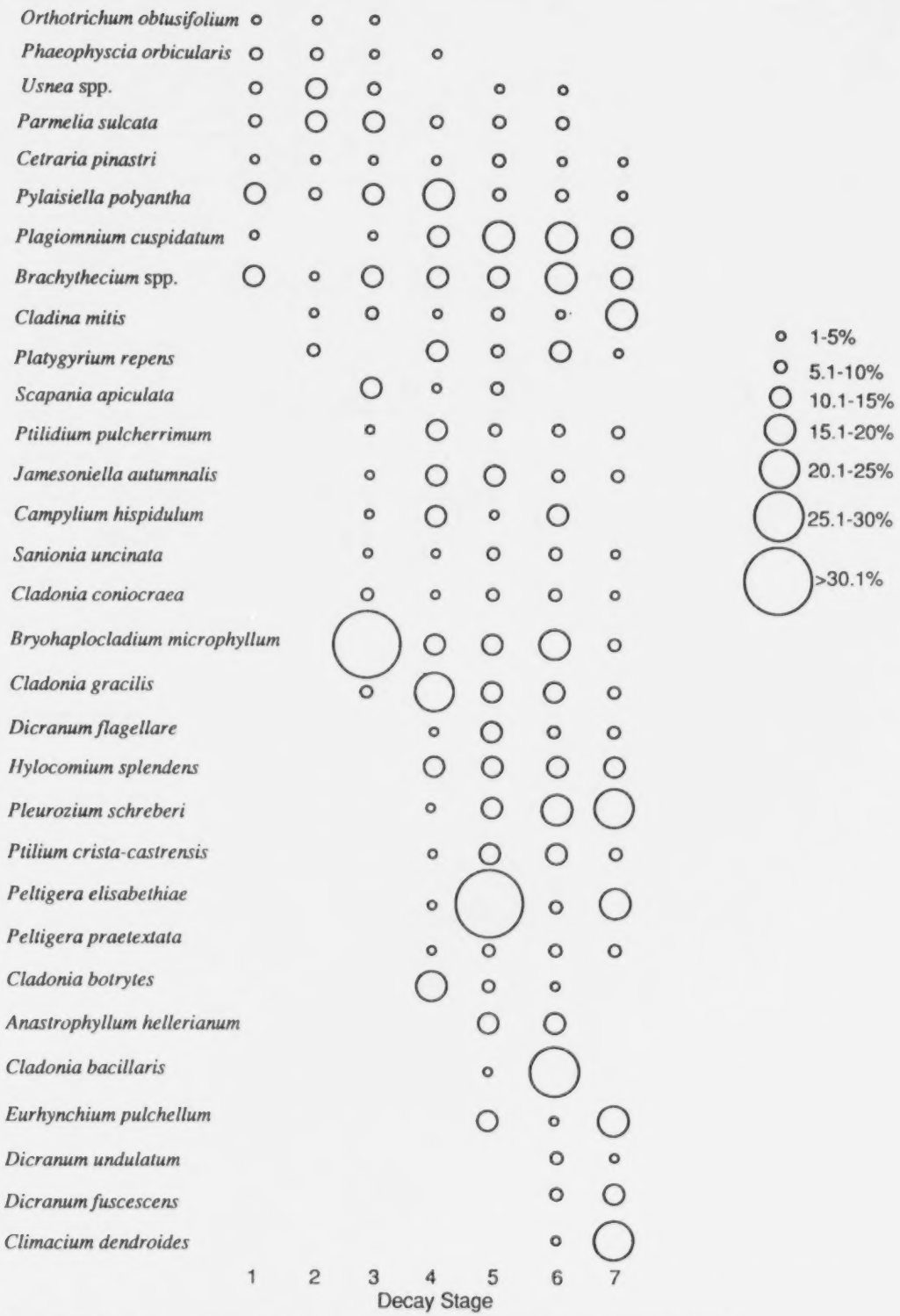

Figure II-13. Percentages of nonvascular species occurring on downed woody material of decay stages one to seven.

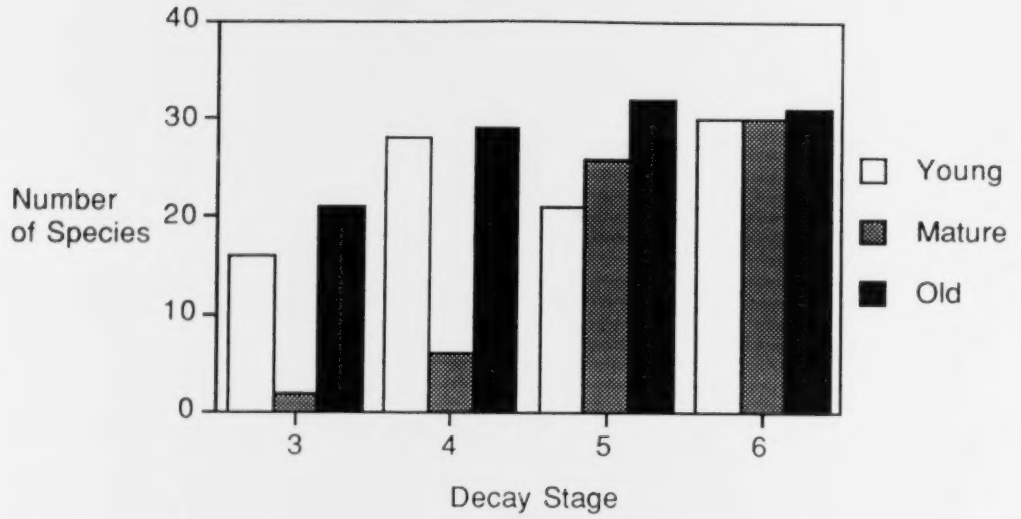

Figure II-14. Nonvascular species richness of decay stages 3-6 across young, mature, and old aspen mixedwood stands. Numbers taken from raw data with unequal numbers of logs within each decay stage. Decay stages 1-2 were omitted due to low sample size of logs, decay stage seven was omitted because significant differences were found between age classes.

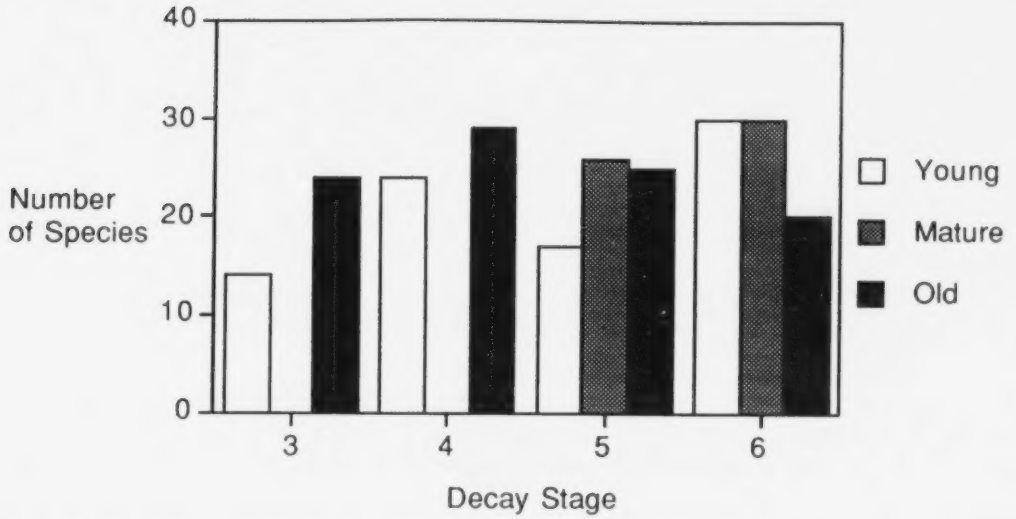

Figure II-15. Nonvascular species richness of decay stages 3-6 across young, mature, and old aspen mixedwood stands. Log numbers within each decay stage were reduced to produce equal sample sizes. Decay stages 1-2 were omitted due to low sample sizes, decay stage seven was omitted because significant differences were found between age classes.

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Chapter III
Environmental Factors of Importance to Some Bryophytes and Lichens on Downed Woody Material in Aspen Mixedwood Forests of Northeastern Alberta

Few investigations have examined the nonvascular plant communities on downed woody material. Most of the investigations, to date, have been on coniferous substrates in the United States (Harmon *et al.* 1986, Harmon 1992) and Sweden (Söderström 1988a, 1988b, 1989). With the exception of one study, there have been no investigations of the bryophyte and/or lichen community on deciduous logs. Andersson and Hytteborn (1991) examined bryophyte communities on a variety of log species, some of which were *Populus* species, however no multivariate analyses of the community were performed. The lack of investigations on deciduous logs have been supported by some investigators stating that deciduous logs are not substrates commonly occupied by mosses and lichens (Lambert and Maycock 1968, Oechel and Van Cleve 1986).

Few studies have been successful in separating out the importance of different environmental factors to nonvascular plant distributions on logs. The difficulty in assessing the importance of certain environmental factors on the nonvascular plant distribution is compounded by the fact that the vegetation itself acts as an integrator of these factors (Jesberger and Sheard 1973). Most environmental variables are treated as continuous variables. Difficulties arise when studying the effect of environmental variables on epiphytic vegetation. The major influencing variable on epiphyte distribution is the host substrate, which itself is a discontinuous variable (Jesberger and Sheard 1973).

Successional studies of mosses and lichens on standing live trees have been extensive (see Jesberger and Sheard 1973, McCune and Antos 1982, Stone 1989, Hyvärinen *et al.* 1992, McCune 1993, Hilmo 1994). Many investigators have agreed that, on standing trees, succession was influenced by the physical changes of the substrate, structural changes within the forest, and many other co-varying factors such as light, humidity, and climate (Jesberger and Sheard 1973, McCune and Antos 1981, Söderström 1988a). Successional studies of nonvascular species on coniferous logs have documented a sequence that begins with fungi, followed by lichens and hepatics, then mosses, and finally herbs, shrubs, and/or tree seedlings (McCullough 1948, Muhle and LeBlanc 1975). More work needs to be carried out, particularly on deciduous logs, to understand how mosses and lichens use the logs, and in what successional sequences. Urgency of the need for such information in Alberta is due to the advent of large-scale

hardwood harvesting in northern Alberta. Both scientists and managers need to know what assemblages of previously undocumented nonvascular plant species rely on these hardwood forests of northern Alberta, to be able to make informed management decisions regarding the maintenance of these species in our managed forests.

The purpose of this study was to determine whether there was a detectable successional pattern of commonly occurring lichens and mosses on downed logs as they decayed in aspen mixedwood forests. If so, what were the main determinants of the successional pattern. Variables such as light, pH, decay stage, wood type, and stand age were determined and subjected to multivariate analysis with species data using canonical correspondence analysis (CCA).

Methods

For a detailed description of the study area, see Chapter II.

In 1992, 836 logs were sampled and placed into one of seven decay stages (Chapter II). A log was defined as any piece of downed woody material greater than 11 centimetres in diameter. In 1993, a random subset of these logs were selected within each decay stage in half of the stands that were sampled in 1992, totaling 132 logs. Decay stages ranged from one to seven, with stage one representing a freshly fallen tree and stage seven representing a log almost completely decomposed. Logs sampled in 1992 were found in four young (23-26 years), four mature (51-63 years), and four old (122-146 years) stands of aspen mixedwood forest. Two stands of each age class were used for this study. Six sites (100 metre radius) were selected within each age class, for a total of 36 sites where downed logs were sampled. For this study, logs were randomly selected based on decay stage, not stand age. Based on data collected in 1992, the maximum possible number of logs were sampled within each decay stage, up to 30 logs/decay stage.

Logs were located by extending transects from the centre of each site, to the corresponding direction and distance that a particular log was located at the previous year. Because logs were selected within decay stages, if there was not a log visible at the coordinate, the nearest log of the same decay stage was selected.

Variables such as pH, percent canopy openness, and type of log (deciduous or coniferous) were recorded for the random subset of logs during July and August, 1993. All species were recorded along the length of each log within 25 centimetres on either side of the transect. Environmental variables were measured at the point where the transect intersected the log.

pH. On logs, pH was measured by digging a one to three centimetre well, depending on the hardness of wood, with a pocket knife into each log sampled. Distilled water was poured into the well and was allowed to equilibrate for two minutes. pH paper (colorpHast® Indicator Strips pH 0-7) was submersed in the water for two minutes. The pH paper was then removed and pH to the nearest half unit was recorded. This technique was initially tested in the lab with a pH meter, and results were comparable.

Canopy cover. Canopy cover above each log was analysed using a hemispherical photographic technique. Hemispherical photography is a technique that can trace different solar paths on a photograph, and then the total radiation summed for the day, week, or year. Photographs were taken with the camera placed directly on the surface of the log and leveled. Photographs were taken using a 15 mm 74° lens. Each picture was taken using fine-grained black and white film (TMAX-400, Kodak Inc.). All exposures were under-exposed by an average of two stops to achieve sufficient contrast between sky and foliage. Photographs were digitized and analysed for percentage canopy openness using Solarcalc (Chazdon and Field 1987).

Wood Type. Wood fragments were taken from each log and examined with a monocular field microscope. If vessel elements were present, wood was categorized as deciduous; if vessel elements were absent, wood was categorized as coniferous.

Vegetation. For each log sampled, presence or absence of wood, bark, moss species, lichen species, herbs, and tree seedlings or coppices, were recorded. These variables from hereon will be referred to as species variables, and the logs from which they were sampled are the sample variables. Due to time constraints both in the field and in the lab, only the most common species of bryophytes and lichens were identified and some species that were unidentifiable in the field were grouped into genera. Nomenclature follows Anderson *et al*. (1990) for mosses, Egan (1987, 1989, 1990, 1991) for lichens, and Moss (1983) for vascular plants. For this study the term "nonvascular" refers to bryophytes, lichens, and fungi; algae were not included in this study.

Data Analysis

Ordination was used to examine the relationships of the measured environmental variables with the species distributions. Species were ordinated with correspondence analysis (CA) and canonical correspondence analysis (CCA) using CANOCO version 3.11 (ter Braak 1987a, 1990). Standard default options were used. The axis eigenvalues generated by CA and CCA were compared to determine whether or not the environmental variables measured were sufficient to explain the major floristic gradients in the data (ter Braak 1987b).

The data set consisted of presence/absence of species variables on sampling units (logs). Environmental variables included decay stage (from one to seven), stand age (young, mature, or old), pH, high light and low light measurements, and the nominal variable of wood type (deciduous or coniferous).

Ordination arranges sites along axes based on data of species composition. For the first axis, CCA selects the linear combination of environmental variables that maximize the dispersion of the species scores (ter Braak 1987b) The second and further CCA axes also select linear combinations of environmental variables that maximize the dispersion of the species scores, but remaining axes are uncorrelated with previous CCA axes (ter Braak 1987b). The result is a biplot that portrays the relationship between species and environmental variables.

A Monte-Carlo permutation test (ter Braak 1990) was performed to investigate the statistical significance of the relationship between the species data matrix and the environmental data matrix. The first eigenvalue was used as a test statistic with 99 permutations.

Results

Logs were unevenly sampled within stand age and decay stage. There were 36, 37, and 59 logs sampled in young, mature, and old stands, respectively, and 5, 11, 14, 21, 23, 29, and 26 logs sampled within decay stages one through seven, respectively. Decay stage one represents a freshly fallen tree and decay stage seven represents a log almost completely decomposed (see Chapter II for details). In total, there were 13 mosses, 13 lichens, and four tree species recorded (Table III-1).

Environmental variables

Percent canopy openness varied with stand age. Light measurements in young stands were higher, on average, and had the greatest range than the other two age classes (Table III-2). Mature stands experienced the lowest percent canopy openness, as well as the narrowest range in percent canopy openness (Table III-2).

Log pH increased with stand age for both deciduous and coniferous wood types (Table III-2). Mature stands had the highest percentage of coniferous logs (35%), while both young and old stands had the same percentage (14%). Coniferous logs had a lower pH on average (4.1) than deciduous logs (5.3), although the total number of coniferous logs encountered was low (Table III-2).

Correlations between environmental variables

There were correlations in pairwise comparisons between environmental variables (Table III-3). The strongest positive correlation (with the exception of the nominal variable of wood type, which exhibited a perfect negative relationship) among the environmental variables was between pH and woodtype. Decay was negatively correlated with stand age and percent canopy openness. pH was positively correlated with stand age (Table III-3).

Correlations between environmental variables and ordination axes

There was a significant relationship between the species distributions and the environmental variables measured ($P = 0.01$, Monte Carlo test). CA based on 132 logs and 30 species variables had four important ordination axes, indicated by high eigenvalues (Table III-4). CCA generated high species-environment correlations of 0.89, 0.67, 0.55, and 0.53 for the first four ordination axes, respectively. Eigenvalues of CA compared to CCA, together with the species-environment correlation, indicate that environmental variables measured were sufficient to explain some of the variation in the species data. CCA had a dominant floristic gradient indicated by a high eigenvalue on the first axis (0.64) compared to axes 2, 3, and 4 (Table III-4).

Species were distributed along one dominant ecological gradient on the first CCA axis. By examining canonical coefficients that define the first two axes and correlations of environmental variables with these axes, decay stage showed the strongest correlation to the first axis (Table III-5). Canonical coefficients define the axes as linear combinations of environmental variables (ter Braak 1987a, b). Correlations of environmental variables with the axes are termed intra-set correlations. Intra-set correlations are correlation coefficients between environmental variables and ordination axes (ter Braak 1987b). By examining the signs and relative magnitudes of canonical coefficients and intra-set correlations, the relative importance of each environmental variable for predicting community composition can be determined (ter Braak 1987b). When environmental variables are strongly correlated with one another, their relative effects on community composition cannot be determined, leading to unreliable canonical coefficients. However, intra-set correlations do not have this problem, and are therefore reliable for interpretation of correlated environmental variables (ter Braak 1987b). In these data, wood type had a perfect negative correlation, because there are only the two categories. This creates the problem of multicollinearity in the canonical coefficients for woodtypes, therefore only intra-set correlations should be used for interpretation of this category (Table III-5). The second axis had the strongest correlation to pH, age, and

wood type (Table III-5). The first two CCA axes accounted for 71.2% of the variation in the data.

Species-environment biplot

The species-environment biplot permits assessment of relationships between species and environmental variables. In the ordination diagram of Figure III-1, species are represented by points and environmental variables are represented by arrows. Species points, together with environmental arrows, reflect the distribution of species along each of the environmental variables. Each arrow represents an axis that is obtained by extending the arrow in both directions (ter Braak 1987b). The direction that the arrow of an environmental variable points is the direction of greatest variation in that variable. The relative length of an arrow is a measure of how much the species distributions differ along that variable. The longer an arrow, the stronger the correlation of that variable to the ordination axis (ter Braak 1987a). To determine how a species relates to a particular environmental variable, a perpendicular line is projected from the species point onto the line of the environmental variable. This allows one to assess the correlation of each environmental variable with each species. If the projected points of the species fall on the middle of the environmental axis, the species are either unaffected by that variable, or they are responding to intermediate values of that variable.

Relationships between species and environmental variables can be interpreted from Figure III-1. Nominal environmental variables for wood type, 'conif' (coniferous) and 'decid' (deciduous), are represented by their respective centroids. Decay, as mentioned, is the major determinant of axis 1. Axis 2 is primarily determined by pH, with age and wood type also being correlated (Figure III-1). Most of the species (or species variables) to the left of the origin are associated with logs that are in more advanced stages of decay, such as *Pleurozium schreberi*, *Ptilium crista-castrensis*, and *Hylocomium splendens*. Conversely, species (or species variables) on the right of the origin are associated with logs that are in intermediate to low decay stages, such as *Xanthoria polycarpa*, *Parmelia sulcata*, and *Usnea* spp. (Figure III-1). Species variables on the lower half of the ordination diagram, such as *Physcia adscendens*, *Picea glauca,* and *Phaeophyscia orbicularis* appear to be associated with more alkaline sites, older aged stands, and are more likely to be found growing from deciduous logs. The environmental variables of age and wood type are correlated with pH, explaining this trend further. *Aulacomnium palustre*, *Cetraria pinastri*, and *Hypogymnia physodes* are associated with more acidic sites, and tend to be found on coniferous logs in younger aged stands (Figure

III-1). Mosses are restricted mostly to the left side of the diagram and lichens are mostly on the right.

Discussion

Environmental Variables

Canopy cover. Percent canopy openness was highest in young stands and lowest in mature stands (Table III-2). These results were expected due to the successional pattern in aspen mixedwood stands. Young stands received more light due to the shorter trees and less dense canopy than in older age classes. The canopy was relatively closed in mature stands, as evidenced by the lowest light levels. Old stands had slightly higher light levels than mature stands.

To optimize carbon gain, mosses and lichens are adapted to seasonal fluctuations in light, water, and temperature (Hicklenton and Oechel 1977, Kershaw 1977). Habitat can influence species photosynthetic responses. Therefore, species found growing in a shaded environment may have low light compensation requirements (Oechel and Sveinbjörnsson 1978, Sveinbjörnsson and Oechel 1992). One might assume that a strategy of mosses and lichens of deciduous understory environments, such as in this study, is to reach optimum photosynthetic capacity in early spring before leaf-out. However, there are many discrepancies in the literature regarding the optimum season of photosynthesis for nonvascular plant species of deciduous understory environments. In addition, there have been few investigations into the photosynthetic process of understory bryophytes and lichens. On live trees, Hosokawa *et al.* (1964) found corticolous mosses and lichens in beech forests had maximum photosynthetic rates in late summer, and species growing further down on a tree had a net reduction in photosynthesis at high light values. Kershaw and MacFarlane (1980) examined thalli of *Peltigera praetextata* and *P. scabrosa* of understory environments. Both species of *Peltigera* were able to acclimate to low light levels and maintain a given level of photosynthetic capacity. Lichens in more northerly environments exhibited acclimation of optimum photosynthetic levels in response to temperature in June and July (Kershaw 1985). Hicklenton and Oechel (1977) found that radiation levels required to saturate the photosynthetic process of *Dicranum fusescens* growing in an arctic environment were optimal in mid summer. Laboratory exposure of *Dicranum fusescens* to high light intensities in the spring resulted in a net reduction in photosynthesis. Kershaw (1985) summarized the discrepancies and lack of concrete results on seasonal changes in photosynthetic capacity as a complex interaction between light, temperature, and moisture. He further suggested that an underlying

biological mechanism controls the seasonal timing of photosynthetic capacity in lichens, which we have yet to understand.

However, in contrast to evidence of optimal photosynthesis for mosses in late summer, other researchers have found the photosynthetic rate of lichens to be higher in the spring and fall (Smith 1961). Temperatures are optimal for photosynthesis in summer, however, drought may influence levels of photosynthesis (Hale 1974). Hale (1974) suggested that lichens may be bimodal in their assimilation, occurring primarily in spring and fall. Dilks and Proctor (1975) found mosses and lichens to be most sensitive to desiccation in autumn and early winter with their tolerance increasing through the spring to a maximum in early summer. More research needs to be completed in this area, specifically in the boreal mixedwoods, because there is a correlation between habitat of mosses and lichens and degree of drought resistance (Hale 1974). It would have been of value in this study to obtain light measurements in spring, before leaf-out, to discern if the higher light levels found during spring may be more important in controlling species distribution than summer light levels.

pH. Wood decay fungi are known to acidify their growth medium (Rayner and Boddy 1988, Zabel and Morrell 1992). Rayner and Boddy (1988) report the average pH range for *Populus tremuloides* logs is 4.2-5.8. Similarly Alban and Pastor (1993) found the average pH of aspen logs after being on the ground for 11-17 years was 4.67. It is important to note that in these studies the pH was determined from processed wood tissues taken from inside logs. pH measured on the outside of the log or bark will likely be different that the pH measured inside the log. Internal pH measurements are misleading because both brown- and white-rot fungi lower the pH (Rayner and Boddy 1988, Jurgensen *et al*. 1989). I could find no literature documenting changes in surface pH of deciduous logs as they decayed.

Standing live deciduous trees have been examined extensively. Culberson (1955) found bark pH, when combined with moisture retention and hardness of the bark, was a major influence on the distribution of lichens between deciduous and coniferous species. Generally, conifers have lower bark pH than deciduous trees (Hale 1974). However, pH values can vary greatly between trees of the same species, and even between different levels on a tree trunk. The difference in pH between coniferous and deciduous trees can help to explain the epiphytic distribution on downed logs of early decay stages. These data can not be extrapolated to more advanced decay stages because information is not available regarding the possible influence of leaf litter, moss and lichens, and precipitation on the pH of deciduous logs. Furthermore, the presence of lichens on trees can modify the tree pH. Kershaw (1964) found uncolonized areas of trees to have a

lower pH than colonized areas. Jesberger and Sheard (1973) sampled 169 *Picea glauca* trees and found average bark pH to be 4.55. In the same study, 113 *Populus tremuloides* trees were found to have an average bark pH of 5.55. My data indicate the average pH of deciduous logs in decay stages one, two, and three was 5.7, 5.0, and 5.0, respectively. The pH of 5.7 for logs in decay stage one is not reliable because there were only three deciduous logs in this decay stage; decay stages two and three had nine and 12 deciduous logs, respectively. The average pH of coniferous logs was 4.5, 3.5, and 3.3 from the first three decay stages respectively (taken from two, two, and three logs, respectively). The small numbers of logs in the early decay stages of this study does not allow a comparison to Jesberger and Sheard's study, however these results fall into the ranges found by Jesberger and Sheard (1973), with the exception of the coniferous logs being more acidic.

Stand Age. Many environmental variables were correlated. Age and pH were positively correlated. However, there were unequal number of logs sampled across the age classes (Table III-2). When logs numbers were equalized across age classes (n = 24 in each age), there was little change in pH (5.0, 5.3, and 5.3 in young, mature, and old stands, respectively).

Older forests have more humid microenvironments than younger forests (Franklin *et al.* 1981, Lesica *et al.* 1991). This high humidity is thought to be caused by greater amounts of water-holding woody debris and a deeper tree canopy in old stands (Franklin *et al.* 1981). Logs found in old stands were in a greater variety of decay stages and had bigger diameters than logs found in young stands (Chapter II). The greater abundance of rotting wood will increase the humidity in the understory as the decay process increases the moisture content of wood (Harmon *et al.* 1986, Mattson *et al.* 1987). One could extrapolate then, and suggest that mosses and lichens associated with older stands are responding to a moisture gradient as well as a time gradient. The moisture gradient allows these species to become established, while the time gradient allows them to increase in abundance and increases the probability of random colonization events.

Decay. Decay is negatively correlated with stand age, and uncorrelated with pH. This means that more logs were sampled in earlier decay stages in older stands than were sampled in young stands. This does not reflect the true ecological relationship because logs were selected with the criteria of fitting into particular decay stages, and we have already seen (Chapter II) that, when randomly sampled, young stands had more logs in earlier decay stages than old stands.

As it is, the data of this study indicates there is no relationship between decay stage and pH (Table III-3); however the same unequal sampling effort that was biasing the pH and age data could be biasing this relationship. Other researchers have found a

negative relationship between coniferous logs and decay stage (see Harmon *et al.* 1986). When equal numbers of logs are sampled across decay stages (n = 9 in each decay stage, except for stage one due to low numbers), there was no change in the relationship. Values for pH across decay stages with equal sample sizes were 5.0, 5.1, 5.1, 5.1, 5.3, and 5.2, for decay stages two through seven, respectively. Therefore in deciduous logs examined in this study, there was no relationship between pH and decay stage of the logs. Coniferous logs can not be equalized in this way because numbers are too low (Table III-2).

The process of wood decay is complex and highly variable. Rate of wood decay varies with species and wood type, colonizing organisms, temperature, and moisture (Swift 1977, Harmon *et al.* 1986, Mattson *et al.* 1987). Wood density and carbon decrease, and respiration, nutrient content, and moisture content increase with increasing decay (Harmon *et al.* 1986, Mattson *et al.* 1987). Deciduous logs generally decay more rapidly than coniferous logs (Harmon *et al.* 1986, Alban and Pastor 1993, Arthur *et al.* 1993), although little information is available on decomposition of deciduous logs (Alban and Pastor 1993). There are higher percentages of sapwood, which is living tissue, in deciduous logs compared to coniferous logs. Living tissue is easier to decay due to the high concentrations of readily disposable materials such as sugar, starch, and protein (Harmon *et al.* 1986). The vessel elements of deciduous logs have a larger diameter than tracheids of coniferous logs and form a more continuous pathway through the wood, making deciduous logs more susceptible to rapid fungal colonization (Harmon *et al.* 1986). This faster decay rate of deciduous logs makes comparisons of colonizing species between deciduous and coniferous wood types difficult. Coniferous logs will be in the environment longer, allowing for more opportunities of colonization and growth of nonvascular species.

A significant relationship between measured environmental variables and species distributions was demonstrated. Decay stage probably indirectly reflects some of the microclimatic variables found in aspen forests, such as moisture. The measured environmental variables accounted for some of the variation in the species data. This could be the result of modest variation in some of the measured variables, for example, exact ages of the stands were not entered into the ordination. Furthermore, some important environmental variables were not measured, e. g., moisture. The high eigenvalues of the CA analysis indicated there was high variation in species distributions. Much of the variation could be the result of random dispersion of spores, gemmae, soralia, isidia, and fragments (Hilmo 1994).

Ecological groupings

Some important ecological relationships can be inferred from the ordination diagram (Figure III-1) and the correlations (Table III-5). Ordination axis 1 is a strong decay gradient, while axis 2 is mainly a pH gradient, on which the more basic sites are older and have a higher percentage of deciduous logs and a lower percentage of coniferous logs. Of the four quadrants in Figure III-1, each contains a group of species variables that represents a successional pathway that is determined by log decay, pH, and stand age. Two of the quadrants contain pioneer species, with one quadrant having species variables associated with younger, more acidic stands and the other quadrant having species variables associated with older, more basic stands. There are also two climax groups that have the same associations with stand age and pH as the pioneer groups. Perhaps an unmeasured moisture gradient is related to stand age, explaining the two colonizing and climax groups.

Quadrant I. Quadrant I contains species variables of wood, bark, *Pylaisiella polyantha, Orthotrichum obtusifolium, Phaeophyscia orbicularis, Melanelia exasperatula, Physcia adscendens, Physcia aipolia,* and *Xanthoria polycarpa,* and *Ramalina dilacerata. Ramalina dilacerata* and *Physcia aipolia* were present on three logs or fewer; therefore may be present in quadrant I due to chance. Species in quadrant I are associated with logs in very early decay stages that are basic, in older aged stands, and are deciduous. Freshly fallen logs in older aged stands are likely from an older cohort of trees than logs in any other age class. It follows then, that epiphytic lichens of old stands that are associated with this type of log, have had sufficient time to colonize and become well-established on previously live trees. These species may represent a climax epiphytic community that occurs on older trees in aspen stands that is not seen in younger stands. Epiphytes that are associated with young stands (quadrant II) may be related to the microclimate found there. On the other hand, such epiphytes may be out-competed by the climax community that is found in older stands. Laundon (1957, in Hale 1974), described a "union" which included *Xanthoria* and *Physcia.* This "union" was characterized by species found on neutral or basic barks in habitats receiving heavy supplies of nitrates. It follows then, than pH could serve to discriminate the preferences of these species for logs of early decay stages in old stands; however the pH did not appear to change with stand age in this study.

Another previously reported association within quadrant I is between a species of *Orthotrichum, Physcia aipolia,* and a species of *Ramalina.* Söderström (1989) found these species occurring together on coniferous logs and characterized them as early pioneers. It is interesting that they are associated more with old stands than young stands

in these data, perhaps reflective of different successional communities between aspen and coniferous logs, or different microclimatic regimes between the two forest types. However, Söderström (1989) did not examine different seral stages.

Quadrant II. Species within quadrant II form the second pioneer group (the first being species variables within quadrant I). *Usnea* spp., *Parmelia sulcata*, *Hypogymnia physodes*, and *Cetraria pinastri* are associated with logs in early decay stages, that are slightly acidic, and are found in younger aged stands. There are two exceptions to these generalized preferences. *Parmelia* and *Usnea* are associated with logs in earlier stages of decay than *Hypogymnia* and *Cetraria*, whereas the latter two species are associated with logs that have a lower pH than logs the former two are associated with species. The measured environmental variables serve nicely to explain this group. Laundon (1957, in Hale 1974) characterized *Parmelia sulcata*, *Usnea* (*subfloridana*), and *Hypogymnia physodes* as being in constant association, an association that is characterized by acidity and sunny habitats. It should also be noted that light levels are weakly increasing in the same quadrant of the ordination diagram where these species occur (Figure III-1), and percent canopy openness was highest in young stands. Similarly, Söderström (1988b) found *Hypogymnia and Cetraria* more abundant on early decay stages on spruce logs in Sweden, and Stone (1989) found *Hypogymnia, Parmelia sulcata*, and *Usnea* among the earliest colonizers of oak trees in Oregon. Stone (1989) also reported that *Usnea* decreased in abundance through time, and speculated that this was due to increasing humidity of the microenvironment with stand age.

Quadrant III. This quadrant contains species that are generally unaffected by the environmental variables that define the second axis, with the exception of *Aulacomnium palustre* which was associated with more acidic substrates in younger aged stands. In addition to *Aulacomnium palustre*, this quadrant consists of *Betula papyrifera*, *Pleurozium schreberi*, and *Ptilium crista-castrensis*. *Oncophorus wahlenbergii*, *Polytrichum juniperinum*, and *Abies balsamea* were present on only three logs or fewer; therefore their placement within the ordination is not accurate due to the low variance in their response to the measured environmental variables. The mosses of this group, with the exception of *Aulacomnium palustre*, dominate in the understory of spruce forests, therefore this can be considered a climax community (Andersson and Hytteborn 1991). Söderström (1988b) found this group of mosses, together with *Cladina rangerifera*, tolerant of dry conditions and were able to colonize spruce logs early but did not dominate until advanced stages of decay. Similar associations between species in this group suggests they constitute a climax community that is tolerant of higher light and lower humidity than the proposed climax community of that will be discussed below.

Young stands had the highest percent canopy openness, and many of the species of quadrant III are associated with this seral stage.

Quadrant IV. This quadrant consists of Herbs, *Populus tremuloides, Picea glauca, Brachythecium* spp., *Bryohaplocladium microphyllum, Plagiomnium cuspidatum, Hylocomium splendens, Sanionia uncinata,* and *Thuidium recognitum. Populus tremuloides* and *Thuidium recognitum* were present on only three logs or fewer, indicating their presence within this quadrant could be due to chance. Species in this quadrant are either associated with logs that are in more advanced to intermediate decay stages or are unaffected by decay. They also are associated with deciduous logs that are neutral to slightly basic in pH and in mature to older aged stands. Andersson and Hytteborn (1991) found *Sanionia uncinata* and species of *Brachythecium* to be part of a group they referred to as opportunistic generalists. These species are generally found on a variety of exposed substrates, but do not persist on well-decayed logs. It is unexpected for *Hylocomium splendens* to be associated with this group because most literature reports *Hylocomium* colonizing from the ground and persisting until the log has decayed (Söderström 1988b, Andersson and Hytteborn 1991). It could be that in the aspen mixedwood system of this study there are two climax groups consisting of species within quadrants I and II (see below), depending on the microclimate or substrate.

Tree Seedlings

Downed logs are important sites for seedling establishment (Harmon 1989, Harmon and Franklin 1989). Nakamura (1992) and La Roi and Stringer (1976) reported that bryophytes, feathermosses specifically, provided safe microhabitats as seedbeds of vascular plants. Bryophytes have the ability to maintain a relatively humid environment and to act as a protective cushion which can reduce the impact of damage from herbivores and rain (Black and Bliss 1980, Cross 1981). However, mosses have also been thought to intercept nutrients from above and absorb them, making these nutrients unavailable to vascular vegetation (Sveinbjörnsson and Oechel 1992). Further, as mosses decompose, these nutrients are released in more usable forms, to be easily absorbed by vascular vegetation. Söderström (1988a) found that the rough texture of a log surface could aid in trapping seeds. It follows, then, that as logs decompose and become fragmented, the suitability for colonization increases. A log colonized by mosses and lichens would also provide a rough surface, in addition to moisture, facilitating seed germination and creating organic soils as the nonvascular species decayed (Harmon 1989).

Birch and aspen seedlings, or copices, were found on more advanced decay stages (Figure III-1). However, birch seedlings were associated with more acidic substrates than aspen, and aspen was found in older stands than was birch. Moore (1985) found that when compared to soils from birch sites, aspen soils had a more favorable chemical environment for microbial activity due to increased exchangeable bases, increased cation exchange capacity, elevated soil pH, and a greater moisture content. Both species need high moisture conditions for germination, which could have been provided by the mosses they were found growing amongst. Balsam fir, on the other hand, can tolerate a lower pH than aspen or birch and is shade tolerant (Corns and Annas 1986). Environmental variables that balsam fir was associated with in this study can not be accurately determined as only one seedling was found.

Bryophytes are important for the survival of spruce seedlings (Nakamura 1992). Spruce seedlings can tolerate acidic substrates for germination and growth, as can many mosses and lichens (Nienstaedt and Zasada 1990). Spruce seedlings in this study, however, were found on deciduous logs having a basic pH in older stands. This can be explained by stand age. As aspen stands age, spruce develops in the understory, increasing in frequency and abundance. It follows, then, that most of the spruce seedlings found in this study were in old stands. Most of the spruce seedlings that were observed in old aspen stands were found on downed logs (Crites, pers. obs). Old aspen stands will have more deciduous logs than coniferous logs in the understory because the dominant canopy tree is aspen. As I have demonstrated, the pH of deciduous logs was not acidic, therefore spruce seedlings must take advantage of available habitat to establish. Conifer logs are naturally more acidic than deciduous logs (Jesberger and Sheard 1973). In this study, however, there was a low representation of conifer logs. Therefore, we can not say that because we found more spruce seedlings on deciduous logs, which are naturally more basic, that spruce prefer this substrate. The literature suggests the reverse is true (Harmon *et al.* 1989).

Lichens are generally first to colonize a live tree, and will remain on the bole once the tree has become a log. As the environment changes, however, such as habitats that experience shading, litter accumulation, or unstable substrates, the communities are eventually replaced by bryophytes and higher plants (Hale 1974). The successional trend in this study as determined by decay began with epiphytic lichens in early decay stages, followed by epixylics such as liverworts, then terricolous species such as feather mosses were abundant in more advanced stages of decay. Decay was the major environmental variable that determined the above trend; however, pH, age, and wood type were also weaker determinants. If age is positively correlated with moisture, the second axis may

also be determined by moisture. This theory is supported by the species distributions on the second axis; species associated with drier sites were located on the upper half of the ordination and species associated with moister sites were located on the lower half of the diagram. The higher canopy openness measured in young stands also supports this theory.

Table III-1. Codes and percent occurrence on logs (n = 132 logs) of species variables included in the analysis.

Species Variable	Code	%
Mosses		
Aulacomnium palustre (Hedw.) Schwaegr.	Aul pal	3.0
Brachythecium spp.	Bra spp	35.6
Bryohaplocladium microphyllum (Hedw.) Wat. & Iwats.	Bry mic	21.2
Hylocomium splendens (Hedw.) Schimp. *in* B.S.G.	Hyl spl	13.6
Oncophorus wahlenbergii Brid.	Onc wah	0.8
Orthotrichum obtusifolium Brid.	Ort obt	12.9
Plagiomnium cuspidatum (Hedw.) T. Kop.	Pla cus	22.7
Pleurozium schreberi (Brid.) Mitt.	Ple sch	24.2
Polytrichum juniperinum Hedw.	Pol jun	2.3
Ptilium crista-castrensis (Hedw.) de Not.	Pti cri	18.2
Pylaisiella polyantha (Hedw.) Grout	Pyl pol	13.6
Sanionia uncinata (Hedw.) Loeske	San unc	5.3
Thuidium recognitum (Hedw.) Lindb.	Thu rec	0.8
Lichens		
Cetraria pinastri (Scop.) Gray	Cet pin	9.1
Hypogymnia physodes (L.) Nyl.	Hyp phy	3.8
Melanelia exasperatula (Nyl.) Essl.	Mel exa	
Parmelia sulcata Taylor	Par sul	19.7
Phaeophyscia orbicularis (Necker) Moberg	Pha orb	
Physcia adscendens (Fr.) H. Olivier	Phy ads	3.0
Physcia aipolia (Humb.) Fürnr.	Phy aip	1.5
Ramalina dilacerata (Hoffm.) Hoffm.	Ram dil	0.8
Usnea spp.	Usn spp	12.9
Xanthoria polycarpa (Hoffm.) Rieber	Xan pol	3.4
Tree seedlings		
Abies balsamea (L.) Mill.	Abi bal	0.8
Betula papyrifera Marsh.	Bet pap	8.3
Picea glauca (Moench) Voss	Pic gla	3.8
Populus tremuloides Michx.	Pop tre	
Other categories		
Bark	Bark	9.1
Herb spp.	Herb	46.2
Wood	Wood	8.3

Table III-2. Mean, minimum (min.), and maximum (max.) values of the environmental variables of light measurements in the understory; and pH for the nominal variables of coniferous (conif.) and deciduous (decid.) logs, for young, mature, and old aspen mixedwood stands. Light was measured as percent canopy openness. Values in parentheses are the total number of logs found in that category.

	Young			Mature			Old		
Variables	mean	min.	max.	mean	min.	max.	mean	min.	max.
light	29.9	14.7	93.4	21.8	12.3	33.1	26.0	13.2	41.6
pH									
conif.	3.5 (5)	3	4	3.9 (13)	3	5	4.8 (8)	3.5	6
decid.	4.9 (31)	3	6	5.1 (24)	3	6	5.9 (51)	4	6

Table III-3. Pairwise correlations (Pearson) between environmental variables before calculation of ordination axes.

	decay	pH	age	light -low	hard -wood	soft -wood
decay	1.00					
pH	0.03	1.00				
age	-0.26	0.26	1.00			
light -low	-0.28	-0.11	-0.09	1.00		
deciduous	-0.05	0.53	0.07	0.01	1.00	
coniferous	0.05	-0.53	-0.07	-0.01	-1.00	1.00

Table III-4. Eigenvalues generated by four ordination axes of CA (Correspondence Analysis) and CCA (Canonical Correspondence Analysis).

	Axes			
	1	2	3	4
Eigenvalues CA	.82	.69	.66	.57
Eigenvalues CCA	.63	.28	.14	.10

Table III-5. Canonical coefficients and intra-set correlations of environmental variables with the first two axes of CCA for nonvascular plant distribution on logs.

Variable	Coefficients		Correlations	
	Axis 1	Axis 2	Axis 1	Axis 2
decay	-1.02	-0.16	-0.99	-0.07
pH	0.13	-0.36	0.09	-0.77
age	-0.09	-0.51	0.21	-0.61
light-low	-0.02	0.18	0.26	0.31
deciduous	0.02	-0.48	0.14	-0.69
coniferous	0.00	0.00	-0.14	0.69

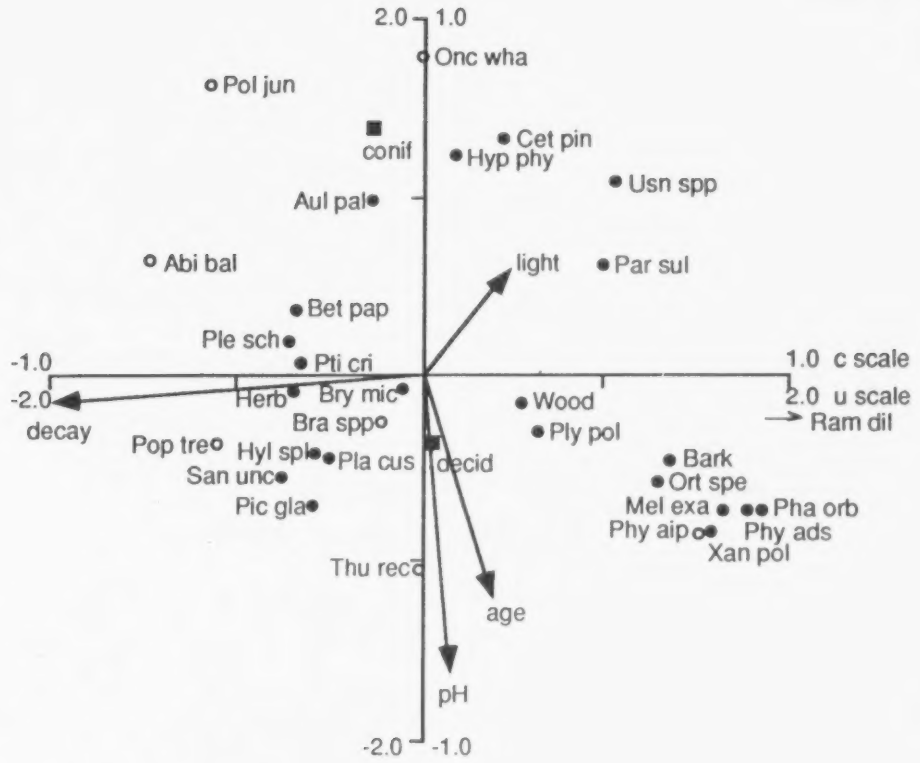

Figure III-1. Species-environment biplot for axes 1 and 2 of a CCA ordination. Positions of species variables (moss and lichen species, tree seedlings, bark, and wood) are shown by open circles for species found on three logs or fewer, and closed circles for species with a greater cover value. Environmental variables are represented by arrows pointing in the direction of maximum variation and squares represent the centroid positions for the nominal variables of deciduous and coniferous logs. The *c* scale applies to environmental variables, the *u* scale to species variables. Codes for species variables are presented in Table III-1.

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Chapter IV
General Discussion

This study documented assemblages of bryophytes, lichens, and fungi on downed woody material, and the interactions of these species with their environment. My specific objectives were: a) to determine whether richness and abundance of nonvascular species, and the diversity of their corresponding substrates changed with forest seral stage and downed log decay stage (Chapter II), and b) to determine whether there were detectable patterns in the distribution of bryophytes and lichens on downed logs, and whether this pattern could be explained by environmental factors (Chapter III).

My principal conclusion in Chapter II was that bryophytes, lichens, and fungi changed in richness and abundance with stand age and decay stage. The substrates that bryophytes and lichens were growing on also changed with stand age and decay stage. There were more species found in old stands than in other ages, and many of these species were rare. There were distinct visible differences among the decaying wood on the forest floor, allowing for classification into one of seven decay stages. The distribution of these substrates also changed with seral stage of the forest. Younger seral stages were characterized by downed woody material in early stages of decay and of small diameter. Mature stands were characterized by downed woody material in advanced stages of decay and of large diameter. Old stands were characterized by downed woody material of all decay stages and a wide range of diameters. These results are important because downed woody material in all stages of decay provide a number of different substrates that are critical in maintaining a rich nonvascular plant flora (Söderström 1988a, 1988b, Andersson and Hytteborn 1991, Selva 1994), and many nonvascular species have been found only on wood of large diameters (Söderström 1988a, 1988b, Andersson and Hytteborn 1991). Selva (1994) found rare indicator lichen species required forests old enough to acquire the variety of microhabitats that enabled these rare species to become established. Once the rarer species are established, Selva (1994) maintains that they require substrates in various stages of decay to ensure survival within these old forests.

Another important conclusion from Chapter II was that a significant amount of the variability in nonvascular plant distributions can be explained by the variance in bark, wood, and herb variables recorded from downed logs. These three variables serve to separate early decay stages from later decay stages. The fact that nonvascular species

could not be used to discriminate between decay stages further emphasized the intergradation that occurred among downed log decay stages.

In Chapter III, my conclusions were that a portion of the variability in the distributions of bryophytes and lichens could be explained by decay stages of the logs, and to a lesser extent by pH, stand age, and the type of wood (deciduous or coniferous). Bryophytes and lichens were grouped into ecological associations that depicted a successional trend as the logs decayed. This pattern was characterized by epiphytic lichens on early decay stages. The composition of this pioneering community varied depending on stand age and/or log pH. Intermediate decay stages were characterized by epixylic liverworts and mosses. Advanced decay stages had feathermosses and other terricolous nonvascular species associated with them. The climax community found on logs of more advanced decay stages also varied depending on age of the stand and/or pH of the log. As with pioneering groups, there was a climax group that was associated with younger stands and more acidic substrates and a climax group associated with older stands and more basic substrates. A similar, although completely descriptive successional pathway was presented in Chapter II. The environmental variable that regulated the differences among pioneering groups and climax groups was likely moisture. Forest stands increase in humidity as they age due to the amount of woody material, which increases in moisture with decay, and the increased canopy depth (Harmon *et al.* 1986, Mattson *et al.* 1987). Therefore, depending on the age of a stand and the decay stages available for colonization, different species may colonize logs and form one of two possible climax communities. These results serve to explain the variation detected in the species distributions in Chapter II. No distinct species assemblages were detected and a significant amount of overlap was found (Chapter II). Two different species groups both colonizing and then dominating the logs would make it difficult, if not impossible, to distinguish between these groups with the analysis used in Chapter II (discriminant analysis).

Recommendations for Logging

To ensure the survival of nonvascular plant communities in Alberta's boreal forest, careful management needs to be implemented. Old aspen mixedwood stands are of particular concern due to the factors mentioned above and because they will be brought into rotation first. Managers need to ensure there is adequate representation of old aspen mixedwood stands in a given area at a given time. One thing we cannot tell managers is how many stands are needed, how big they need to be, and in what proximity to each

other. Our lack of knowledge in these areas emphasizes the need for conservative management.

Given what we know about dispersal of bryophytes and lichens, juxtaposition of stands should be an important consideration. For a species to persist in an area, extinctions must be equal to colonization and dispersal from outside. Therefore, old stands should not be isolated, that is, they should be surrounded by stands of different ages, not just young stands. It has been demonstrated by Gustafsson (1994) that young stands are not useful for dispersal, likely because they are not useful for colonization. If an older stand is surrounded by a clear-cut, species within the old stands will not be able to disperse outside the stand. One conclusion by Gustafsson *et al.* (1992) was that small areas of old forest can be more important as dispersal sources than larger areas of young forest. It follows that to ensure survival of nonvascular plant populations, suitable substrates need to be available, old age classes need to be present, and old stands should not be completely isolated.

We do know that old aspen stands have unique assemblages of nonvascular species that are not entirely related to structural attributes. Therefore, recreating old stands by leaving structure on cutblocks, or by speeding up succession by planning for high structure in younger aged stands, may be insufficient to ensure survival of these plant communities. Some old aspen mixedwood stands should be allowed to escape harvest to serve as ecological bench marks and source areas for maintenance of this nonvascular plant component of diversity. In the future, some forests that have been harvested should be allowed to develop to old ages before the next cutting. These managed forests should be closely monitored to determine whether maintenance of stand structure in the form of downed logs in cutover areas is sufficient to allow recolonization by rare nonvascular species.

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Appendix. Relative proportions of lichens, mosses, fungi, and liverworts occurring on downed woody material in young, mature, and old aspen mixedwood stands in northeastern Alberta. These data were used in Chapter II.

	Young	Mature	Old	Total
Lichens				
Cetraria pinastri	0.71	0.06	0.19	0.97
Cladina mitis	0.61	0.15	0.03	0.79
Cladonia bacillaris	0.29	0.05	0.00	0.33
C. botrytes	1.10	0.03	0.00	1.13
C. cenotea	0.00	0.01	0.00	0.01
C. chlorophaea	0.00	0.06	0.13	0.19
C. conoicraea	0.67	0.73	0.83	2.24
C. crispata	0.00	0.05	0.00	0.05
C. fimbriata	0.06	0.00	0.05	0.11
C. gracilis	3.62	1.81	0.24	5.67
C. multiformis	0.34	0.00	0.05	0.39
C. pyxidata	0.19	0.00	0.00	0.19
Cladonia spp.	0.33	0.40	0.56	1.29
Evernia mesomorpha	0.00	0.00	0.10	0.10
Hypogymnia physodes	0.05	0.00	0.02	0.07
Parmelia sulcata	3.65	0.15	2.24	6.04
Peltigera aphthosa	0.26	0.13	0.00	0.40
P. canina	0.97	0.13	0.31	1.40
P. didactyla	0.17	0.05	0.10	0.31
P. elisabethiae	0.14	0.41	1.01	1.56
P. evansiana	0.00	0.00	0.14	0.14
P. membranacaea	0.14	0.05	0.00	0.19
P. neckeri	0.10	0.19	0.05	0.33
P. neopolydactyla	0.09	0.00	0.00	0.09
P. praetextata	0.92	0.63	0.67	2.22
Peltigera spp.	0.05	0.04	0.05	0.14
Physcia adscendens	0.00	0.00	0.10	0.10
Usnea spp.	0.55	0.02	0.47	1.04
Xanthoria polycarpa	0.00	0.00	0.05	0.05
Phaeophyscia orbicularis	0.12	0.00	0.53	0.66
White crustose lichen	0.00	0.00	0.06	0.06
Lichen spp.	0.67	0.00	0.27	0.94
Mosses				
Amblystegium serpens	0.11	0.00	0.05	0.15
Amblystegium varium	0.00	0.00	0.15	0.15
Aulacomnium palustre	0.72	0.17	0.00	0.89
Brachythecium spp.	11.76	6.47	21.99	40.21
Bryoaplocladium microphyllum	3.16	3.60	14.97	21.73
Campylium chrysophyllum	0.00	0.00	0.16	0.16
Campylium hispidulum	0.47	0.00	0.40	0.87

	Young	Mature	Old	Total
Mosses cont'd.				
Ceratodon purpureus	0.03	0.03	0.00	0.06
Climacium dendroides	0.00	0.00	0.32	0.32
Dicranum flagellare	0.07	0.87	0.30	1.24
D. fragilifolium	0.00	0.06	0.00	0.06
D. fuscescens	0.00	0.68	0.16	0.83
D. polysetum	0.00	0.12	0.00	0.12
D. undulatum	0.00	0.21	0.13	0.34
Eurhynchium pulchellum	0.43	0.11	0.25	0.79
Hylocomium splendens	1.14	2.12	1.82	5.08
Oncophorus wahlenburgii	0.37	0.18	0.08	0.63
Orthotrichum obtusifolium	0.00	0.03	0.55	0.58
O. speciosum	0.00	0.00	0.11	0.11
Plagiomnium cuspidatum	1.99	4.06	19.00	25.06
P. ellipticum	0.00	0.03	0.00	0.03
P. medium	0.09	0.00	0.00	0.09
Platygyrium repens	0.11	0.33	1.35	1.78
Pleurozium schreberi	2.94	12.65	2.58	18.17
Pohlia nutans	0.03	0.21	0.02	0.26
Polytrichum juniperinum	0.00	0.11	0.00	0.11
Ptilium crista-castrensis	2.74	3.10	0.80	6.64
Pylaisiella polyantha	2.84	0.76	1.64	5.24
Sanionia uncinata	0.48	0.40	1.19	2.06
Tetraphis pellucida	0.00	0.05	0.00	0.05
Thuidium recognitum	0.00	0.00	0.36	0.36
Fungi				
Armillaria mellea	0.04	0.00	0.00	0.04
Bjerkandera adusta	0.00	0.00	0.26	0.26
Crepidotus mollis	0.17	0.00	0.00	0.17
Calcium spp.	0.00	0.00	0.12	0.12
Didymium squamulosum	0.00	0.00	0.03	0.03
Fomes fomentarius	0.00	0.00	0.04	0.04
Hyphodermella corrugata	0.00	0.00	0.21	0.21
Hypoxylon multiforme	0.00	0.00	0.11	0.11
Lamproderma arcyrioides	0.05	0.00	0.00	0.05
Lycoperdon perlatum	0.00	0.00	0.03	0.03
Phellinus tremulae	0.00	0.00	0.05	0.05
Physarum sp.	0.00	0.00	0.05	0.05
Pseudorhizina sphaerospora	0.00	0.00	0.03	0.03
Schizophyllum commune	0.10	0.00	0.00	0.10
Stemonitis axifera	0.00	0.02	0.00	0.02

	Young	Mature	Old	Total
Fungi cont'd.				
Stemonitis fusca	0.03	0.00	0.00	0.03
Trametes hirsuta	0.00	0.00	0.17	0.17
Trichaptum abietinum	0.00	0.00	0.13	0.13
Tricharpum biformis	0.00	0.00	0.51	0.51
Fungus spp.	0.18	0.00	0.25	0.43
Liverworts				
Anastrophyllum hellerianum	0.00	0.00	0.26	0.26
Geocalyx graveolens	0.00	0.08	0.00	0.08
Jamesoniella autumnalis	0.00	0.99	0.82	1.81
Lophocolea heterophylla	0.05	0.00	0.11	0.16
Ptilidium pulcherrimum	0.29	0.43	0.91	1.63
Riccardia multifida	0.00	0.00	0.02	0.02
Scapania apiculata	0.14	0.00	0.31	0.46
Liverwort spp.	0.13	0.03	0.19	0.35